JOURNAL OF AGRICULTURAL RESEARCH

VOL. XXVIII WASHINGTON, D. C., JUNE 7, 1924 NO. 10

INDIVIDUAL AND AGE VARIATION IN MICROTUS MONTANUS YOSEMITE[1]

By A. BRAZIER HOWELL

Scientific Assistant, Division of Biological Investigations, Bureau of Biological Survey, United States Department of Agriculture

INTRODUCTION

While engaged in field work in Mono County, Calif., during July, 1922, the writer found that it was a year of extreme abundance for the common meadow mouse (*Microtus montanus yosemite* Grinnell), which inhabits the open meadow land of this region, and decided to make a detailed study of the individual and age variation occurring within this single unit group of this genus. A large series of specimens was carefully collected for this purpose.

It seems remarkable that despite the great activity displayed in the study of mammals in America during the past several decades no one has attempted a really comprehensive investigation to ascertain the amount of age and individual variation normal to any single group of small mammals. J. A. Allen (*2*)[2] published a short paper on the subject in 1894, and almost every reviser of a genus or group has done what he could to gain an understanding of these differences; but usually the material available has been of such a nature that no detailed and intensive study in this regard was practicable. Almost without exception series have been small, or, if large, the specimens were secured by different collectors; they came from different, even though closely grouped spots; their histories were not perfectly known; or they were collected with no view to a later study of a particularly intensive nature.

The purpose of the present contribution is twofold—to furnish a detailed report of the above nature and to offer a fairly comprehensive study of the osteology of the skull of a small rodent that is not particularly specialized. Only the exterior aspects of the bones are treated, with the purpose of filling a long-felt need that every systematic mammalogist has experienced at some point in his career. Throughout the discussion the writer has endeavored to treat fully all details that might be considered in any way important; but an effort has been made to avoid lengthy discussion of minute variations which are regarded as relatively unimportant and which would prove most tedious to the reader, and from which more pertinent matter might be separated only with considerable difficulty.[3]

[1] Received for publication Apr. 14, 1924—issued Nov., 1924.

[2] Reference is made by number (italic) to "Literature cited," p. 1015.

[3] The drawings, except those of the muscles and of the foot, were made by the writer. All details comprising each figure are enlarged in the same proportion, but there was no effort to have the various separate figures on the same scale. All numbers of specimens herein mentioned relate to serial numbers in the writer's private collection.

MATERIAL

The series herein discussed is from Long Valley, Mono County, Calif. Here, at an altitude of 6,800 feet, Convict Creek meanders through miles of open, marshy, pasture land to join near by the upper reaches of Owens River. The conditions at this spot are very uniform. The trapping ground was far from any other association (except dry sage), and the growth, although exceedingly lush, consisted almost wholly of a half dozen predominating grasses and small sedges, with the local Iris in drier situations. As there are here few *kinds* of foods, there can not be great variation in the shaping influences that particular fare may have upon various parts of the skull. It is known that the stresses and strains developed by the different major muscles of the skull have the greatest influence upon its exact configuration, and much—perhaps most—of the individual variation therein is probably due to such cause. Where great diversity of food, such as grains, grasses, alfalfa, root crops, fruit, and the like, is available, there must be a corresponding diversity in the developmental stimuli of the skull muscles, according to whether an animal lives in a situation where one or another type of food predominates. In the Long Valley association such variety of food is practically at a minimum.

Disturbing influences as well are here very slight. The topography precludes the danger from severe floods, while the presence of the snow-fed creek, coupled with the fact that a part of its waters are so led as constantly to irrigate the meadows, minimizes the possibility of pronounced drought. Too, there is ample range for cattle in the valley, so that there is no overgrazing, with consequent destruction of favorable cover. Hawks are very few, and local indications suggest that the only furred predatory animals likely to exact appreciable toll upon the mice would be an occasional foraging coyote or mink. The only mammal which could compete with them ecologically to the slightest extent is the small shrew *Sorex vagrans amoenus*, which uses the runways of the rodents. Hence, theoretically, the meadow mice lead an existence that is unusually free from erratic influences, where all must eat substantially the same fare, and we are justified in assuming that there occurs less than the usual amount of individual variation among the specimens themselves.

From July 9 to 17, 170 voles were trapped within a territory extending along the bank of the creek for about one-third of a mile. Of these, all specimens with damaged skulls and a majority of the juveniles were discarded. Each specimen retained was weighed and carefully relaxed by manual manipulation before taking the three measurements of total length, tail, and hind foot. The mammae were then examined and notes taken on the number and size of the tubercles upon the soles of the hind feet. While skinning the specimens, observations were made upon the development and condition of both the outer and inner surfaces of the hip glands and upon the number and size of embryos when present. The skulls, after being labeled, were immersed in water to draw the blood, usually for 48 hours; the brains were then removed by syringing and placed in a 70 per cent solution of alcohol.

Forty-eight hours before cleaning, the skulls were placed in water, and were then heated in a solution of soap, soda, and ammonia, the cooking having been regulated with such care that it was possible to bring them to a point at which the saponified flesh could be removed by means of a fine stream of water without recourse to scraping or brushing, hence obviating the usual danger of damaging the finer processes while manipulating the scraper and brush. There has thus resulted a series consisting of 66 skins with skulls, besides a number of alcoholic specimens, collected within nine days in virtually the same spot by a single collector. In addition, every skull has been *thoroughly* cleaned and is perfect

down to the smallest detail (save for the lachrymals), except for four that were very slightly damaged by the traps.

Of this series but three specimens are definitely juvenile, the remainder being adults and subadults, all sexually mature. Such maturity can at once be distinguished in the field by an experienced collector, but not with certainty in the case of prepared specimens. Criteria are the general appearance of the animal before skinning, the condition of the pelage, and the development of the external genitalia. That such intangible points may be trustworthy in this regard is indicated by the fact that a majority of the very smallest females that are here designated as subadult contained embryos.

These 66 skins with skulls consist of 25 males and 41 females. Unfortunately no record was kept concerning the sexes of the discarded individuals, and it is now impossible to state whether the relative proportion of the two sexes in the series at hand is representative of conditions in the colony at large. The writer would be exceedingly loath to adopt the hypothesis that female Microtus substantially outnumber the males at birth, without evidence of a very conclusive character. Reference to field notes shows, however, that any disparity between the sexes in the series of different species of microtines that the writer has prepared has almost always been in favor of the females. This state of affairs can neither be ignored nor settled offhand.

METHODS EMPLOYED

In addition to extremely careful ocular comparison of the specimens, elaborate measurements of skulls have been taken by means of dial calipers of great accuracy. A list of skull measurements was selected which it was thought, after some trial, might prove to be of greatest value in the study of the subfamily Microtinae. These were made, tabulated according to sex, and arranged consecutively in descending sequence with reference to the condylo-basilar length as a basis. Taking the skull of the female with greatest condylo-basilar length as representing 100 per cent, and each of the other measurements of this skull as also representing 100 per cent, a list of percentages was made, tabulated, and plotted. It was thought that the actual plotting need be done only in the case of the more numerous sex. In the graph for body measurements and weights (fig. 2), also arranged according to the condylo-basilar dimension of the skulls, the averages for both sexes of the three body measurements and the weights have been taken as 100 per cent, each for its respective part.

This treatment of measurements—plotted by percentage and proportion—is believed to give a much clearer perception of the relation of each dimension to every other one considered than does the usual treatment of the subject. The one objection to this method is that in reducing, or rather magnifying, to percentage such small measurements as interorbital width, the coefficient of error is also necessarily magnified; but, nevertheless, such treatment allows one more easily to discern whether there be any correlation between the variations of the various portions of the skull.

It is perhaps too trite to be worth stating that no series of animals can ever be exactly uniform, for there exist too many developmental factors to permit precise correlation between parts, save in very rare instances; hence, all that is possible is an attempt to locate correlative trends between various portions of the animal.

In the accompanying graphs a mean or average line plotted between the perpendicular extremes would represent variation with age, while the extent to which the lines for each sex deviate from such an imaginary mean would signify individual variation.

COLORATION

Microtus m. montanus and the subspecies *yosemite* average slightly darker than the general run of western meadow mice. The pelage is of the usual agouti pattern, but its precise color is not of interest here.

Although there is quite a bit of variation in the shade of the pelage among the males, this is not sufficient to make it easy to divide the series of this sex into two lots based on shade alone. They may, however, very readily be divided into two groups, one of which has an appearance rather dilapidated, this being in part due to wear, but to a greater extent to an uneven appearance which may be ascribed to fighting among themselves, as well as to the great prominence of the hip glands. The other group differs considerably in appearance, for although the glands in the larger individuals of this series are just as prominent as in some of the other lot, the skins have a sleeker look, are but little worn, and show practically no sign of fighting.

Of this second group, one specimen is a large, fully adult male in unworn-looking coat, but the remainder are smaller animals which are readily classed as subadults, sexually adult, except in three cases. These latter have a distinct look of immaturity, which consists of an appearance of shortness and compactness of the pelage of the entire body. The largest of these three, though still largely in the juvenile coat, is labeled as being sexually mature; but the other two are definitely juvenile. The pelage of none of these males is excessively worn.

Four of the females have the dorsal surface excessively worn, this being almost black in places. Severe wear results in the tips of a varying proportion of the hairs of the back breaking off, thus exposing to a greater or lesser extent the dark, plumbeous bases. There is considerably more variation of color in the remainder of the female than in the male series, and it is easy to divide them, according to shade, into two well-marked groups, although there are many intermediate examples the allocation of which is arbitrary. One group, very uniform, is of a brighter shade of brownish than the male series. A few of the males have counterparts in shade among the brighter females, but there are a number of the latter brighter than any of the males. The other group of females is exceedingly variable. Although it contains many individuals which might really, with equal propriety, be placed in the "bright-colored group," the series consists essentially of skins with a definitely more grayish cast, rather than a brownish one. The variation present is largely in the amount of gray. The larger, older females are for the most part paler and grayer than are any of the males and are rather uniform in this respect. The larger subadults are more variable, some of them being a trifle more brownish, while others are of a darker gray than the adults, due to an admixture of a greater number of black-tipped hairs. The whole "gray" series grades down to seven individuals which have the appearance of immaturity, being darker dorsally, with shorter, more compact pelage; but only the smallest specimen is definitely juvenile, for five of the remaining six contained embryos. There are a number of specimens, however, which, although with shorter head and body measurements than some of these six, have the type of pelage of the older animals.

In general, the largest specimens have the longest coats, but unless this be new, the hairs of the ventral surface are not relatively longer. Subadults in sleek pelage, even though this be rather short, normally have the longest hairs upon the underparts, and this surface is then correspondingly paler than in the case of individuals in which there has been wearing away of the pale hair tips. Similarly, specimens with palest underparts have a scanty growth of palish hairs upon the under side of the tails, which when worn away, leaves the tail almost black both above and below. The skin of the feet is uniformly sooty, but the hairs growing

upon these members are lighter and somewhat gray. This is longer upon the feet of fully adult examples than upon younger ones, thus causing the feet of mature animals to appear paler.

An arrangement of all males and females in two lots according to sex and with reference to the head and body measurement corroborates, on the whole, the above observations on coloration. The results, however, are not by any means all that could be desired, for probably 25 per cent of the specimens do not occupy the exact positions in the series where one considers, after a very careful study of the pelages, that they should belong. A regrouping of the skins with reference to the condylo-basilar length of the skulls gives results that are much more convincing, and there are then very few of the specimens which seem to belong in other positions. A third regrouping according to weight is a trifle more satisfactory still for males. Weights of females, however, can not be thoroughly uniform with development, because of the frequent presence of embryos. As the difference between these last two arrangements is practically nil, it is perhaps wiser to select the condylo-basilar criterion as the most desirable basis for grouping the skins according to age as indicated by pelage.

TABLE I.—*Measurement of males taken in the flesh, weights, and braincase capacith arranged in descending sequence according to the condylo-basilar measurement of the skulls*

Collection number	Measurements			Weight	Brain-case capacity[a]
	Head and body	Tail	Hind foot		
	Mm.	*Mm.*	*Mm.*	*Grams*	
3835	128	53	23	67.0	130
3837	133	55	22	68.6	120
3812	133	47	23	70.7	109
3826	129	48	21	60.5	128
3833	126	47	23	59.8	114
3825	132	43	22	59.7	113
3834	127	47	22	55.6	106
3822	132	53	22	66.0	119
3818	134	(b)	21	61.4	113
3864	120	48	21	58.8	126
3846	118	49	21	51.0	110
3845	125	47	23	53.2	120
3848	115	55	22.5	45.3	119
3862	120	45	21	48.7	110
3883	120	53	22	49.8	118
3820	122	48	21	47.0	105
3841	113	48	23	42.2	104
3870	116	42	22	46.2	107
3847	111	49	23	43.7	116
3867	115	52	22	45.5	112
3887	110	46	22	35.6	110
3814	111	49	23	38.5	115
3849	111	47	23	43.8	106
3801	117	38	21.5	38.8	99
3857	97	41	22	26.5	96
Averages[c]	122	48.2	22	52.7	113.3

[a] In number of pellets of No. 10 shot.
[b] Tail damaged: Measurement not considered.
[c] Averages of 19 males, the largest two and smallest four specimens being excluded.

TABLE II.—*Measurements of females taken in the flesh, weights, and numbers and size of embryos, arranged in descending sequence according to the condylo-basilar measurement of the skulls*

Collection number	Measurement			Weight	Embryos	
	Head and body	Tail	Hind foot		Number	Size
	Mm.	*Mm.*	*Mm.*	*Grams*		*Mm.*
3815	119	49	21	57.6	8	6
3856	124	46	22	49		
3865	127	48	22	57.7		
3819	121	45	22	56.4		
3844	130	48	22	59	7	3-7
3871	128	50	22	53.6		
3816	121	48	22	54.5	6	3
3845	119	49	22	48.4		
3817	128	47	21	58.5	6	11
3884	123	46	20.5	49.6		
3836	122	46	22	55		
3881	121	47	21	55.9		
3877	118	43	21	49.2		
3863	128	40	22	62.2	8	11
3869	116	47	21	43.5		
3876	123	44	21	55	6	10
3831	121	44	21	45.6		
3821	118	48	22	45.2	5	2
3840	117	50	22	42.2	5	2
3880	118	47	22	46.4		
3830	119	44	21	43.7		
3827	120	47	21	55.1	5	13
3828	117	50	22	47.8	7	6
3872	118	45	22	41.8	3	9
3838	114	49	22	47	7	3
3850	117	50	22.5	46.5	6	5
3885	118	47	21	53.8	4	16
3886	117	47	21	46	5	3
3873	121	45	22	43.9		
3813	118	45	21.5	36.2	5	2
3882	108	45	22	34.8		
3839	106	47	21.5	38.8	4	2
3852	114	48	22	42.3		
3829	118	47	21	42.7		
3842	112	48	21	40.2	3	6
3861	105	46	21	40		
3866	119	42	22	56.7	7	16
3851	115	47	21	48.2		
3888	109	43	21.5	38.7		
3832	98	39	21	29.6		
3833	93	39	21	22.9		
Averages [a]	118.2	46.5	21.6	48.2	5.6	6.9

[a] Average number of embryos of 41 females; average measurements and weight of 32 females; the largest three and smallest six being excluded.

CONCLUSIONS

The pelage of males is comparatively uniform, except that the older ones are rather ragged, chiefly due to fighting. The series of females is much more variable and may be divided into (1) a grayish group which, on the whole, contains a majority of the oldest individuals, many of which are grayer than any male; and (2) a brownish group composed chiefly of smaller subadults, but among which are a number of older individuals. The second group averages somewhat more brownish than the brightest males. Other things being equal, the larger and older the animal the longer the pelage. The feet of adults average paler than those of subadults. Juveniles are characterized externally by a slightly darker appearance and shorter, more compact pelage, although some of this indication of immaturity persists in sexually mature individuals.

A grouping of the whole series with reference either to weight in the flesh or condylo-basilar length of the skull gives results eminently more satisfactory and natural than when they are grouped according to the head-and-body measurement.

MOLT

None of the specimens at hand is conspicuously in molt. In fact, a definite zone of molt such as often occurs in the case of Thomomys seems never to occur among microtines. The same applies to the writer's belief that there is no very definite season for the change of pelage in this subfamily. Individuals apparently molt largely according to age, although there are presumably other factors, chiefly climatic or dietetic, which may accelerate or retard such changes. About the time of sexual maturity there is usually a lengthening and slight brightening of the pelage, apparently due to a gradual growth of new hairs. This seems to begin upon the lower sides and extends upward. In some individuals it is also seen to extend from the face rearward but not at all pronouncedly. In the specimens that are most worn there is no evidence of the growth of new hairs, possibly indicating that such worn condition of the coat is not due to an imminent approach of the molt, but rather to some mechanical agency, or possibly to some pathological condition of the individual. Unfortunately, the writer failed to record, except in the case of a very few of the last specimens, the condition and color of the inner surface of the pelt. Such observations might have proved to be of decided interest.

MAMMAE

All females had eight mammae, there being two pairs inguinal and two pairs pectoral. Some of these, usually the pectorals, were often extremely hard to distinguish in the smaller subadults. It is a well-known fact that not all the mammae may be functional in the case of young animals with small litters; hence the full complement may be correspondingly difficult of definition.

FIG. 1.—Sole of the left hind foot of *Microtus m. yosemite* (No. 3858), showing position of the plantar pads.

PLANTAR TUBERCLES

It seems to have been accepted for years without serious question that species of the subgenus Microtus uniformly and invariably have six tubercles or pads upon the sole of each hind foot. The writer has found that there is much variation in this respect in the case of a number of species, though not all, and variation in the present form proves to be great.

Save in the case of spirit specimens, satisfactory determination of the plantar pattern must be made with fresh material. It is thus possible to compare only such unprepared animals as may be at hand, and it is impossible precisely to carry in one's mind the exact plantar development of the individuals in a considerable series. Hence, it is extremely difficult to record in satisfactory terms the variations which may occur. In the present instance the error must have been appreciable in judging the precise amount of development, whether one should say there were five or six pads upon an individual foot according to whether the sixth was vestigial, small, or medium.

There is considerable individual difference in the development of the tubercles which is entirely independent of age. In some animals they are relatively swollen and well developed while in others they are smaller, though more sharply defined as a usual thing. The general plan consists of a plantar pad upon the sole between, but posterior to, the bases of each pair of toes—four of them, which are designated the anterior ones. In addition, there is situated posterior to the first or antero-medial tubercle—the one between the bases of the hallux and second digit—a fifth tubercle, the postero-medial, which is normally the largest of all, but is variable to some extent. The usual sixth tubercle, the postero-lateral,

when present, is located posterior to the antero-lateral one and is the most variable of all. It may be entirely absent or may vary from vestigial to well developed. The writer's notes show that out of 72 animals preserved 19 had six plantar tubercles; 24 had five; 1 but "four and a half"; while in still another individual there were only four distinct pads, there being but the faintest trace of a fifth. In addition, one animal had six pads on one foot and five on the other. This great variation in plantar pattern is purely individual and probably indicates that the sixth tubercle is in process of being lost; although it is not impossible that the reverse contention is the proper one.

HIP GLANDS

The same difficulty in a study of the hip glands is encountered as when recording data concerning the plantar tubercles, but to even a greater extent, for it is impracticable to examine the inner surface of the pelt of more than one or two animals at a time. This is a very real handicap, especially as the terms employed in describing the glands, such as faint, well developed, or reddish, are necessarily vague.

Externally the glands appear as a pair of patches situated well up on the hips and upon which the hair is more sparse, as well as shorter, than on the remainder of the dorsal surface of the trunk. In the dried skins of large males they are about 20 mm. apart, and as they are thicker than the remainder of the pelt they become considerably harder and less elastic to the touch when dry. These glandular patches evidently consist of groups of greatly developed and specialized sebaceous glands upon which the hair grows with lessened luxuriance. When they are prominent, there is a slight exudation of liquid from them—enough barely to moisten them—but this is not sufficiently oily to mat the surrounding hair to any extent. The writer has always considered that they act as scent glands and, judging from their situation, that they are for the purpose of leaving an odorous trail upon the closely encroaching sides of the grassy runways for the direction of other voles. This, however, is pure speculation. The inner surface of the pelts of old males shows scars about the head and shoulders. There is also a definite zoning of scars in the vicinity of the glands, indicating that these are probably particular targets for the ire of rivals. Similarly, some of the lagomorphs invariably endeavor to bite the testes of an opponent when fighting among themselves.

In a large male of the present series each hip gland measures about 30 mm. in an antero-posterior direction by 18 mm., and they are 20 mm. apart. Upon the inner side of the undistorted pelt they usually are situated wholly posterior to an imaginary line extending between the orifices in the hide originally occupied by the hind legs; but there is some variation in this respect and they may begin as far forward as a point half an inch anterior to such a line, thence extending rearward. When the glands first begin to develop there appears within the area a slight, whitish thickening upon the inner side of the skin, somewhat granular in texture. This increases in size and coarseness with age. In older males it becomes very thick and coarse, somewhat spongy, and at times congested with a conspicuous network of veins upon the inner surface. As this congested condition is found in some males but is absent in others, the writer judges that it not only indicates an increase in the activity of the gland, but that it may also be of a periodic nature and perhaps is dependent upon sexual activity, although this is merely an assumption upon his part.

The glands are usually of full size in adult males and only very slightly smaller in subadults of medium age, although they may be of distinctly finer texture and are probably much less active in the latter. It is odd that the only male of con-

siderable size which had the hip glands but very faintly indicated is the only specimen of the whole series that was in such condition as subsequently to stain the attached label with grease. Interesting inferences may be drawn from this case; but they are all pure speculation. All males except small juveniles have glands that are readily discernible from the inner surface of the pelt, and they apparently begin really to develop at about the time or just before sexual maturity is attained.

Fully adult females usually have hip glands almost as large, though of a finer texture and more poorly defined, than the males; and they never attain the congested condition often found in old examples of the latter sex. As a rule, an old female has about the same glandular development as a subadult male of medium size. There is some irregularity in its shape in females, however, and it may or may not be present to a slight degree in the smaller subadults of the female series.

The fact that both sexes of the present material have hip glands indicates that these do not constitute a secondary sexual character in the usual meaning of the term, although their development is probably directly contingent upon the attainment of sexual maturity by the animals. The definitely slighter development of the glands in females than in males should point to the hypotheses either that this was originally a race in which both sexes were equally well provided with glands, but that the females are now in gradual process of losing them, or else that the females were first glandless, but are now in course of acquiring them.

EXTERNAL MEASUREMENTS

LENGTH OF HEAD AND BODY

The measurement of total length of all animals in the present series was taken in millimeters after manipulation of the specimens so as to obviate to some extent the effect of *rigor mortis*. The measurement was taken in the usual way while stretching the body to a moderate degree, but with more than usual care.

Since collecting this series the writer has experimented with *Microtus californicus sanctidiegae* to ascertain the amount of variation that one might expect to occur in the measurement of total length when this was secured by a single collector. Two specimens were taken from the traps while still kicking and carefully measured as soon as movement had ceased. Their respective lengths were 199 and 178 mm. Twelve hours later, after a cold night and while the bodies were still very stiff with *rigor mortis*, they were manipulated to remove some of the rigidity before measuring; the figures then were 188 and 166 mm., respectively, while at noon, by which time the bodies were entirely relaxed, they measured 194 and 175 mm. It is thus seen that even when the measurement is taken carefully by the same person total length varies more than 5 per cent, according to the length of time that has elapsed between death and time of measuring. There must be at least 5 per cent additional difference in this figure when it is taken by several collectors, making in all a possible error of 10 per cent in the total length as given upon the labels of the average study skin. Add to this the fact that there is certainly more individual variation in this than in any other external measurement and it is evident that this character constitutes a very poor criterion by which to judge the age and development of a specimen. The length of head and body alone is much more reliable, for then there is not added to the coefficient of error for this, that for the length of tail which is especially subject to mutilation. The practice of taking total length, however, is so firmly established among American scientists that it would be difficult to

institute another mode. After all, it is a very simple matter, though perhaps less satisfactory, to ascertain the head-and-body length by subtracting that of the tail from the total length, as has been done in the present instance.

As mentioned previously, an arrangement of the series of skins with reference to the length of head and body does not give results that are as satisfactory as could be desired. Individual variation, of course, can not be escaped, but, still, this arrangement does not appear as natural to the orderly sequence of pelages and cranial development as does the arrangement according to the condylo-

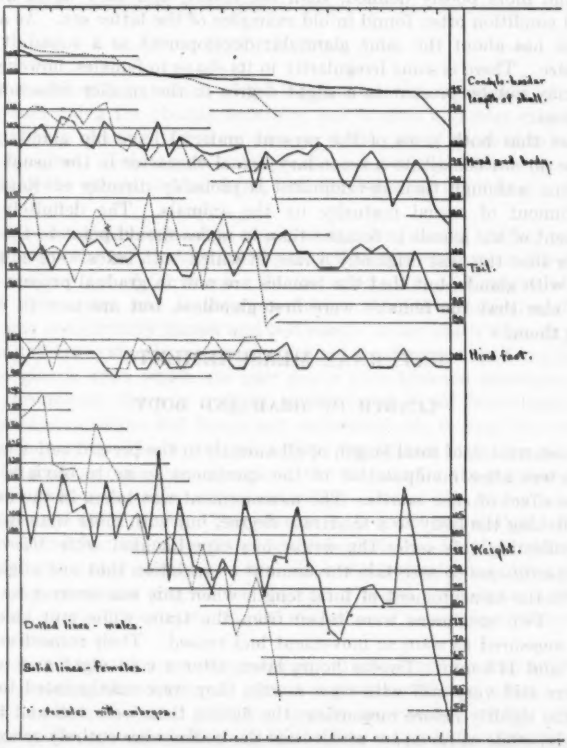


FIG. 2.—Graph showing external measurements and weights of both sexes of *Microtus m. yosemite* reduced to percentages and arranged according to the condylo-basilar length of the skulls, with largest skull of either sex taken as par

basilar length of the skull. When thus disposed, the accompanying graph indicates that there is considerable individual variation; also that the average trend with age is for the head-and-body length to increase at a faster rate than the condylo-basilar length; in other words, the skull of the juvenile is proportionately larger with reference to the body of the animal than is that of the adult, roughly estimated 8 per cent larger. However, this relative disparity practically disappears as soon as sexual maturity has been attained. In taking the average of the external measurements and weights, several of the oldest and youngest specimens, judged by the condylo-basilar dimensions, were eliminated from consideration, even though there are but few in the present series. This was done for the purpose

of obtaining as nearly as possible a correct average of measurement for thoroughly normal, sexually mature individuals of the two sexes. The tables give information that may be desired concerning such specimens as might possibly be considered unusually large adults and juveniles.

For males the average head-and-body length is 122 mm., with extremes of 134 and 110—a difference of 24 mm., or 19.7 per cent of the average. The females average 118.2 mm., with extremes of 130 and 106, again a difference of 24 mm., or 20.3 per cent. The above figures indicate that males are consistently about 4 mm. larger in this measurement than are females, and the writer believes that this sexual difference in size is real, as it is corroborated by other data.

LENGTH OF TAIL

This measurement was secured by placing a millimeter rule at the upper side of the base of the tail of the unskinned animal and then bending this member at a right angle to the axis of the body, measuring to the tip but not including the terminal hairs.

In the case of *Microtus californicus sanctidiegae* it was found that there may be as much as 5 per cent variation in this measurement, depending on the length of time after death that it was taken. Add to this another 5 per cent to account for the different results obtained by various collectors, as well as the fact that throughout life the tail tip is especially subject to injury, and it is evident that this dimension is none too reliable. Extreme variation occurs even in the case of females. In males this measurement should be considered with decided caution, because the tails are so often injured and materially shortened while the animals are fighting among themselves. The average length of tail in males (with oldest and youngest specimens eliminated) is 48.2 mm., with extremes of 55 and 42—a variation of 13 mm., or 27 per cent, of the average. For females these figures are 46.5 mm., with extremes of 50 and 40, showing a variation of 10 mm., or 21 per cent. This difference of 6 per cent in the amount of variation in the two sexes may be partially ascribed to the greater propensity of the males to injury. In both sexes the tail averages 39 per cent of the head and body. Age causes very little variation from this figure. In the case of the six youngest females the percentage rises to 41, but this difference is almost too slight to be taken into consideration.

LENGTH OF HIND FOOT

There is probably less error in measuring the length of the hind foot from the heel to the tip of the longest claw than in either of the other two body measurements. There is little effect of *rigor mortis* upon this member; hence for all practical purposes the same figure will result regardless of how long after death the measurement may be taken, and there need be no difference in the results obtained by various collectors. The normal error in making this measurement, if half millimeters be recorded, will be about 0.4 mm., or slightly less than 2 per cent. In figure 1, of course, this possible error for individuals is magnified almost five times, although the average for the series is not affected.

There is considerable individual variation in the size of the foot, but practically none with age in the specimens at hand. In fact, the 12 largest males have feet that average a shade shorter than those of the 12 smallest; but this difference is so slight (0.1 mm.) that it is of little significance. It will thus be seen that full growth is attained by the feet at an early age, and for this reason foot length often is of much value in identifying juveniles of different species.

The hind foot of males averages 22 mm. in length, with extremes of 23 and 21, a variation of 9.1 per cent of the average; that of females, 21.6 mm., extremes

being 22.5 and 20.5, or a difference of 9.2 per cent. These figures are real and not fortuitous, for there are seven males with a foot length of 23 mm., but no female with feet so long. The individual variation in foot length is considerable, and this measurement may be of only slight diagnostic value when but a few specimens are available; but in series it is important.

LENGTH OF EAR

It is a number of years now since the writer became convinced of the worthlessness of the measurement of length of ear when taken from the fresh specimen in the field. A little experimenting demonstrated that without some sort of apparatus giving an even pull, it is practically impossible for a collector to arrive at any degree of accuracy or uniformity in taking length of "ear from crown," and "ear from notch" is almost as bad in this respect. In fact, the writer obtained some startling results, due to the facility with which the ear tip may be stretched from the head, and he thereupon abandoned the practice of taking this measurement.

In the present study the writer endeavored to use some sort of ear measurement taken from the dried skin, but, because of the usual distortion of this member while drying, has concluded that no reliance can be placed upon any figures resulting, and that it is better to omit this. A careful examination of the ears of the skins at hand indicates that there is no appreciable variation either individually or due to age.

WEIGHT

In any consideration of the weights of mammals one must remember that he is dealing with a measurement of mass, in three dimensions really, whereas all other measurements taken are of one dimension only. It is thus ineyitable that there will be variation of a sharper degree than is usual in measurements of length; but this in itself is no argument against the importance and value of recording weights.

It is not usual for the Microtinae to lay up a great store of fat; in fact it is only rarely, if at all, that any definite quantity of fat is to be found upon them. For this reason the weights of individuals of like size do not fluctuate so decidedly as is the case with mammals which habitually take on a great supply of fat in anticipation of a period of hibernation. The weight of a Zapus taken in fall would be out of all proportion to that of an individual of like age taken in spring. The weight of this sort of mammal is thus of real value only when accompanied by data concerning its condition. The meadow mice of the present series were very uniform in this respect, and almost all contained a moderate quantity of food without having the stomachs greatly distended.

The individual variation in the weights of males is not excessive, considering that this is a measurement of mass. Variation with age is much more pronounced, of course. The average weight of 19 males is 52.7 gm., with maximum of 70.7 for old ones down to 35.6 for small young adults. This is a variation among sexually mature examples of 35 gm., or 67 per cent of the average weight. This amount of variation between individuals of such ages is undoubtedly excessive for rodents in general, but it is a well-known fact that it is usual in this subfamily. In fact, it may sometimes be greater, for veritable giants among meadow mice are not infrequently encountered, although there is none in the series under discussion. It will be noted that the largest male is considerably heavier than any of the females, even than those containing large embryos.

The weights of females are much less reliable and are more variable individually than those of the opposite sex because of the presence of embryos in a large number. The average weight of the 32 females is 48.2, with extremes of 62.2 and 34.8, a difference of 27.4 gm. This size variation among examples that are sexually mature of 56.4 per cent of the average is considerably smaller (11 per cent)

than for males, and if allowance is made for the fact that the three heaviest females were pregnant, the true variation due to age is yet smaller. As the average weight of females is considerably augmented by the presence of large embryos the true difference between the average weights of the two sexes must be considerably greater than the 4.5 gm. shown by the tables.

It is readily apparent that weight is to a large extent correlated with both length of head and body and condylo-basilar length of skull, especially in the case of males; but there is less connection in the female series, complicated as are the weights of many of them by the presence of embryos. There are many exceptions to this rule, however, constituting the normal individual variation.

EMBRYOS

The period of gestation for Microtus, as determined by Bailey (*3*) in the case of the species *pennsylvanicus*, is 21 days. For the first few days after impregnation the embryos are so small as to escape detection by the average collector, who gives but a hasty glance into the abdominal cavity. The writer has no means of knowing the exact time at which appreciable swellings within the uterus indicate clearly that the animal is pregnant, but it is certainly more than three days. If we say three days, to be conservative, then only six out of seven pregnant females are recorded as in this condition by the careful collector. In the present series of 39 sexually mature females, 19, or roughly one-half, were definitely with young. It is entirely possible for meadow mice to bring forth a litter regularly about every 20 days, as determined by Bailey, and although such fecundity is doubtless exceptional in the wild state it probably is closely approached when a period of optimum population among the meadow mice is drawing near. The writer presented data elsewhere (*5*) which have caused him to believe that during the latter stages of and immediately following a peak population of small rodents which fluctuate markedly in numbers during certain periods there is a definite reduction in reproductive power. Indications in the present case, therefore, are that the females were bearing young at neither the maximum nor minimum rates and that the figures here presented are very likely average for meadow mice during midsummer.

The measurements of embryos given are merely for the length of the membranes in which they were contained, not for the total length of the fetus. These measurements vary from 2 to 16 mm., the latter figure being for examples at practically full term and which would probably have been born within 24 hours. Female No. 3844 contained 7 embryos, some of which were 3 and others 7 mm. in length, this variation probably being the result of some pathological condition. The average number of embryos for the pregnant females was 5.6. The 9 largest pregnant specimens contained an aggregate of 56 embryos, or an average of 6.2 each, while the nine smallest held only 44, an average of 4.9. This difference in fecundity according to age may be fortuitous but is probably not, for it is in line with what is known of the subject from experience with domestic animals. The weight of the eight embryos, practically full term, of female No. 3868 (an alcoholic specimen) was 17.3 gm. Only 8 of the 19 largest females contained embryos, while 11 of the remaining 20 subadults were in this condition. These figures may indicate a slight waning of the fertility of some of the oldest individuals.

MYOLOGY OF THE HEAD

The writer thoroughly believes that the development of the skull after birth is chiefly influenced directly by the muscles and their mechanical effects while exerting stresses upon their insertions upon the bones; hence indirectly by the character of the food and feeding habits (including manner of mastication) of the animal.

The juvenile skull is the product of heredity, and there are undoubtedly present developmental factors of one sort or another which contribute toward general trends in certain directions; but the muscles exert powerful strains which can not fail to have the most profound influences in shaping the bones of the young animal. For this reason it is deemed impossible to gain a correct comprehension of the interrelationships and correlations of the different bones of the skull without some understanding of its major muscles, their attachments, and func-

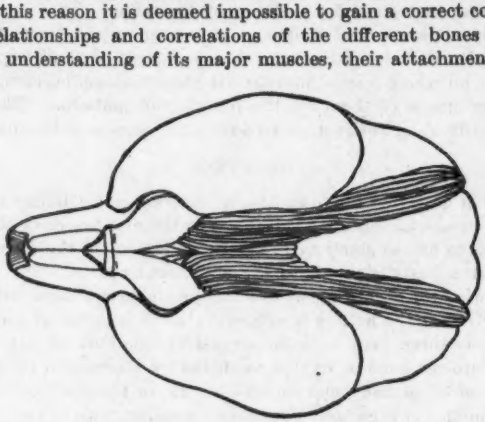


FIG. 3.—Head, showing position of the digastricus muscle

tions (*1*, *4*, *6*, *8*, *9*). The interrelationship of these muscles is so complicated, especially in rodents, that only the main function of each muscle is touched upon here. Although this is not the place for a detailed treatment of the myology of the head, a brief description of the chief muscles used in mastication is deemed

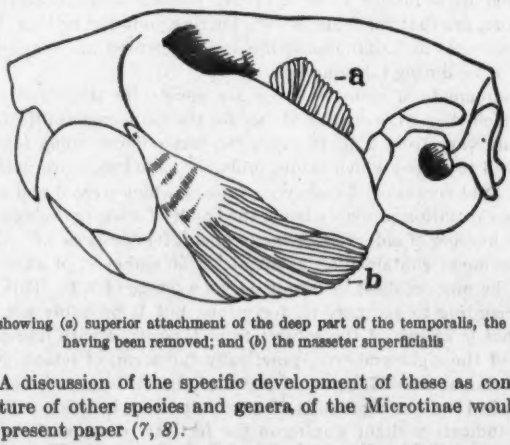


FIG. 4.—Head, showing (*a*) superior attachment of the deep part of the temporalis, the superficial part having been removed; and (*b*) the masseter superficialis

advisable. A discussion of the specific development of these as compared with the musculature of other species and genera of the Microtinae would be out of place in the present paper (*7*, *8*).

DIGASTRICUS.—This arises from the posterior portion of the symphysis of the rami of the mandible, as well as for a millimeter or two upon the inferomedial part of the bone immediately posterior thereto, and extends as a slender band upon either side to insertions upon the paroccipital processes. Its functions are to draw the mandible backward and to open the mouth forcibly, although the latter action ordinarily requires very slight muscular force.

MASSETER.—The chief muscle of the skull and the one most used by the majority of mammals during mastication is the masseter. It is a compound muscle conveniently divided into three parts as follows:

MASSETER SUPERFICIALIS.—This arises from the slightly defined, small process directly below the anteorbital fossa (see fig. 4, *b*), in a stout aponeurosis, which rapidly broadens to form a thin band, developing muscle fibers and extending obliquely rearward to an insertion upon the inferomedial edge of the angular process of the mandible and the portion of the ramus immediately adjacent. The fibers superficial to this insertion are in turn inserted after the usual fashion in the intersection between this muscle and the pterygoideus internus. It is used in drawing the mandible forward.

MASSETER ZYGOMATICA.—This arises (see *b*, fig. 5) by a superficial fascia and deeper muscle fibers upon the inferior portion of the zygomatic arch from the anterior to the posterior angle, but additional strength is secured in this species by the extension of the aponeurotic sheet a couple of millimeters still farther forward along the zygoma, and to this extent it directly overlies a portion of the superficial division of the masseter major. It then descends with a posterior

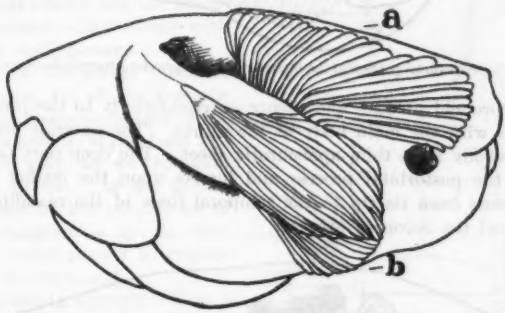


FIG. 5.—Head, showing (*a*) superior portion of the superficial part of the temporalis; and (*b*) the masseter zygomatica (masseter superficialis removed)

trend to an insertion upon the lateral face of the angular process, while a small portion is inserted upon the superior part of the medial face of the same. This muscle is used in closing the jaws, and probably to some extent in pulling the mandible forward.

MASSETER MAJOR.—This is properly divisible into two portions, the pars superficialis and the pars profundus. The former (see fig. 6) arises from the superior edge of the maxillary root of the zygomatic arch, covering the whole anterior face as far as the anterior angle of the zygoma. Its forward bulge covers the anteorbital fossa. It descends with a slight posterior inclination to an insertion upon the masseteric ridge of the mandible. The deep part (see fig. 7), considerably less in mass, arises within the orbit from the posterior edge of the maxillary root of the zygomatic arch, extending backward all along the superomedial edge of the zygoma. There is also a small division, ostensibly of this muscle (the exact status of which, in myomorphine rodents, is a matter of controversy), that arises from the anteorbital fossa and extends through the adjacent foramen to join the main muscle. This deep part is thinly inserted upon the mandible in a line extending from a point upon the lateral face of the ramus directly anterior to the prominence formed by the root of the incisor to the anterior termination of the masseteric ridge. The anterior third of the insertion is purely aponeurotic. The chief use of the masseter major is in closing the jaws, both while gnawing with the incisors and champing the cheek teeth; in addition,

it may be of some help in certain forward movements of the mandible, although this is not the case with many mammals, including man.

TEMPORALIS.—This muscle may also be divided into a superficial and a deep portion. The former (see fig. 5, *a*), well developed in the present animal, arises along the lambdoidal crest and thence forward along the temporal ridge to the posterior termination of the interorbital constriction. It then descends anteriorly and laterally, wholly within the orbit, to an insertion upon the anterior

FIG. 6.—Superficial portion of the masseter major (masseter superficialis removed)

edge of the coronoid process, and thence anteroinferiorly to the junction of the latter process with the main body of the ramus. The anterior portion of the insertion is wholly by a thin, aponeurotic sheet. The deep part (see fig. 4, *a*) arises upon the postorbital process and inserts upon the medial side of the coronoid process from its tip to the temporal fossa of the mandible (between the molars and the coronoid process).

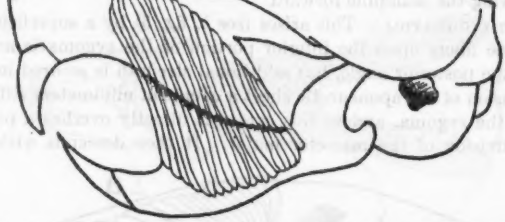


FIG. 7.—Head, showing the deep portion of masseter major, including the anterior portion of the anteorbital branch (masseter superficialis, zygomatica, and the superficial part of major, removed)

The temporal is a very powerful muscle and is used not only for closing the mouth, but to some extent for drawing the mandible backward.

PTERYGOIDEUS EXTERNUS.—This muscle arises from the lateral side of that portion of the external pterygoid plate anterior to the foramen rotundum, and inserts upon the inferior border of the medial process on the head of the condyle.

PTERYGOIDEUS INTERNUS.—This arises from the pterygoid fossa and inserts upon the medial surface of the angular process of the mandible. Both this muscle and the pterygoideus externus are used in lateral movements of the jaw, such motion being produced by their alternate action first from one side then from the other.

THE SKULL

It is necessary to have some criterion on which to base a consecutive arrangement of the skulls for the purpose of study. The most desirable, of course, would be the mean of a variety of characters showing age, such as amount of ridging, angularity, and general development of the skull; but it is impossible for the human eye to appreciate such fine gradations as are involved, and more definite methods must be used. Although some of the smaller skull dimensions might be employed with excellent results, it seems preferable to make use of one of the longer measurements. The total length of skull is perhaps usually favored above all others. In some mammals this measurement is an excellent one, but in others, whose nasals project sufficiently for these to constitute the anterior point of the measurement, it is open to the serious objection that the fragile tips of the nasals are very prone to injury; hence, not only may the skull be damaged to this extent, but the subsequent measurements will fluctuate with the amount of such damage.

The length of the hensel (distance from the inferior lip of the foramen magnum to the posterior margin of the alveolus of the incisor) is free from this objection, and may be an excellent measurement to use. As the precise relative position of the inferior lip of the foramen magnum is apt to vary, however, the writer prefers to employ the following measurement:

CONDYLO-BASILAR LENGTH.—This is the distance from the condyle to the posterior margin of the alveolus of the incisor upon the same side. It constitutes the criterion upon which the arrangement of the present series is based. As previously mentioned, it is the most natural arrangement, when considered with reference to weight and size of the animal and its pelage, that could be devised. The series of skulls thus arranged exhibits a minimum of individual variation.

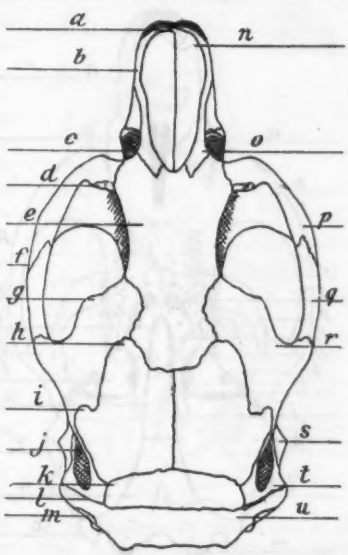


FIG. 8.—Diagrammatic dorsal aspect of skull of adult *Microtus m. yosemite*. *a*, Anterior nares; *b*, premaxilla; *c*, anteorbital fossa; *d*, lachrymal; *e*, frontal; *f*, zygomatic arch; *g*, postorbital process; *h*, anterior projection of parietal; *i*, lateral projection of parietal; *j*, prelambdoidal fenestrum; *k*, interparietal; *l*, lambdoidal crest; *m*, mastoid; *n*, nasal; *o*, ascending branch of premaxilla; *p*, maxillary root of zygoma; *q*, jugal; *r*, squamosal; *s*, audital bulla; *t*, squamosal; *u*, occipital

The skull as a whole is characterized by no marked peculiarities, and its specific characters need not be discussed.

The skull is properly divisible into two parts—the cranium proper and the face. The former should be considered as being made up of three rings as follows: The posterior ring consists of the occipital. In the middle ring are the interparietal, parietals, basisphenoids and alisphenoids, and the temporals, including the squamosals, mastoids, and audital bullae. The anterior ring is formed of the frontals, orbitosphenoids, presphenoids, and the ethmoid.[4] After a fashion, each of these three rings forms an integral part and may be said to vary individually as independently as its articulations with adjoining rings will allow. The face is made up of the nasals, premaxillae, maxillae, jugals, lachrymals, palatines, turbinals,[4] and vomer.[4]

[4] These bones need not here be discussed, as the impossibility of examining them without severely damaging the skull renders them useless as characters in ordinary systematic mammalian studies.

In considering the variation of the skull with age, the anterior ring, chiefly the frontals, of the cranium is "dead center," from which there is development anteriorly and posteriorly. For the purpose of following this general development of the skull with age, there have been selected from the series of females the largest adult, a medium subadult, and the smallest juvenile. The general conclusions reached therefrom have been checked with the remainder of the series, but details regarding only these three will be presented in order to avoid a needless amount of tedious statistical matter. Females were selected in preference to males, because their characters are in most respects more uniform and less extreme.

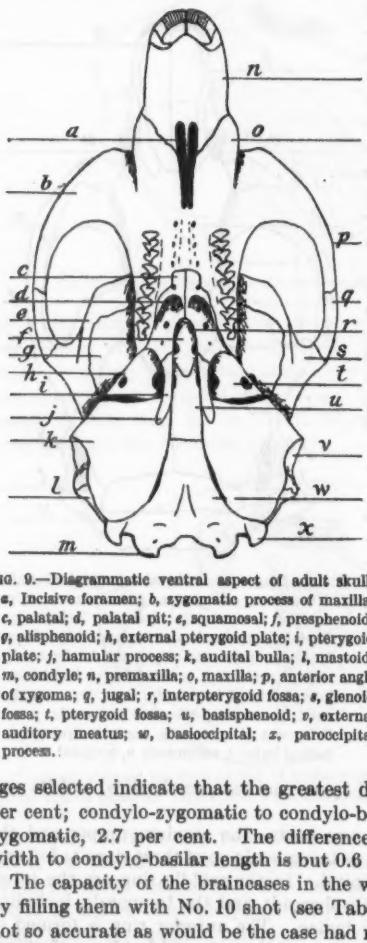


FIG. 9.—Diagrammatic ventral aspect of adult skull. *a*, Incisive foramen; *b*, zygomatic process of maxilla; *c*, palatal; *d*, palatal pit; *e*, squamosal; *f*, presphenoid; *g*, alisphenoid; *h*, external pterygoid plate; *i*, pterygoid plate; *j*, hamular process; *k*, audital bulla; *l*, mastoid; *m*, condyle; *n*, premaxilla; *o*, maxilla; *p*, anterior angle of xygoma; *q*, jugal; *r*, interpterygoid fossa; *s*, glenoid fossa; *t*, pterygoid fossa; *u*, basisphenoid; *v*, external auditory meatus; *w*, basioccipital; *x*, paroccipital process.

Skulls of juveniles are, of course, much weaker than are those of adults. All surfaces are rounded and the processes are more obscure and poorly defined. This is a natural correlation with the weaker, undeveloped condition of the muscle system. In addition, the anteroposterior dimension of the skulls of juveniles have the superficial *appearance* of stubbiness, with relatively much shorter rostrum and diastema, crowded condition of the pterygoid region, and smaller bullae; in transverse dimensions, wider interorbital, narrower zygomatic spread, and wider braincase. A critical study of these points shows that some of the differences enumerated above are merely optical illusions brought about by the lack of strength and ridging and the weak processes of the juvenile skull. In reality, the skulls of the two extremes in age are remarkably and surprisingly similar in relative measurements, as shown both by the figures and camera-lucida studies. In proportion of nasals to condylo-basilar length the three skulls of the ages selected indicate that the greatest difference between them is less than 2 per cent; condylo-zygomatic to condylo-basilar, 1.6 per cent; nasals to condylo-zygomatic, 2.7 per cent. The difference in the proportion of the zygomatic width to condylo-basilar length is but 0.6 per cent.

The capacity of the braincases in the whole series of males was investigated by filling them with No. 10 shot (see Table I, p. 981). The results are perhaps not so accurate as would be the case had mercury been employed, but the difficulty of stopping up all the vacuities and foramina of the cranium rendered the use of this metal impractical. The shot, however, proved satisfactory, and tests have shown that the normal error is only from 1 to 2 per cent. The average capacity of the braincase in the eight normal, adult males with greatest condylo-

basilar length is 115.2 pellets, while that of the eight smallest, normal subadults is 110.3, or 95.6 per cent. A similar comparison of the condylo-basilar length of these individuals gives 91.6 per cent. Comparison of the braincases of the largest superadult and smallest juvenile male results in figures that are misleading (73.8 per cent), for the reason that the brain capacity of the former is abnormally large. Comparison of the average of the three largest specimens with that of the three smallest, however, gives 83.4 per cent, while a similar treatment of their condylo-basilar lengths results in a percentage of 84.5. It is perhaps wiser to ignore the fact that the two latter percentages occur in reverse order to those first stated, for as the difference is small this is very likely due to individual variation. As this latter is considerable, the reader must judge for himself whether the figures indicate true conditions, and whether or not to consider the braincases of the younger animals proportionately larger than those of the older ones. At any rate, this difference with age is assuredly much less than has been popularly supposed. In skulls with the largest braincases the increased capacity is usually due to a slight proportional increase in the length, rather than in the breadth, of the cranium.

Aside from such facts as are offered above, the external surface of the braincase has certain details that do make it appear definitely of greater relative size in comparison with the whole skull in the case of the juvenile. While the condylo-basilar length of the smallest female is 80.8 per cent that of the largest the distance between the prelambdoidal fenestrations of the squamosals is actually 0.4 mm. greater in the juvenile, and the transverse measurement taken between the posterior termination of the postorbital processes is 92 per cent that of the adult. The proportional width (of braincase only) at the zygomatic processes of the squamosals is also about 92 per cent; but this is a very difficult measurement to take with accuracy

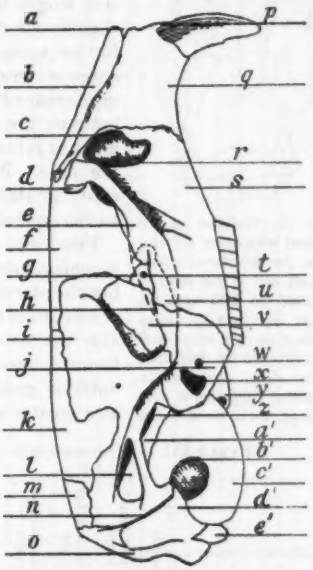


FIG. 10.—Diagrammatic lateral aspect of adult skull. *a*, Anterior nares; *b*, nasal; *c*, anteorbital fossa; *d*, lachrymal; *e*, zygomatic process of maxilla; *f*, frontal; *g*, orbitosphenoid; *h*, sphenoidal fissure; *i*, squamosal; *j*, external pterygoid plate; *k*, parietal; *l*, prelambdoidal fenestrum; *m*, interparietal; *n*, lambdoidal crest; *o*, occipital; *p*, incisive process of premaxilla; *q*, premaxilla; *r*, anteorbital foramen; *s*, maxilla; *t*, optic foramen; *u*, jugal; *v*, alisphenoid; *w*, foramen rotundum; *x*, foramen ovale; *y*, internal pterygoid plate; *z*, premastoid vacuity; *a'*, mastoid; *b'*, external auditory meatus; *c'* audital bulla; *d'*, mastoid; *e'*, paroccipital process.

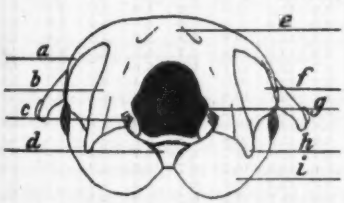


FIG. 11.—Diagrammatic posterior aspect of adult skull. *a*, Lambdoidal process; *b*, exoccipital; *c*, condyle; *d*, basioccipital; *e*, supraoccipital; *f*, mastoid; *g*, foramen magnum; *h*, paroccipital process; *i*, audital bulla.

The interorbital width varies practically none at all with age, and as it is therefore proportionately so much greater in young examples, it adds much to the short appearance of the skull. Still another contributing cause is the weakness of the zygomatic processes of the maxillae in very young animals.

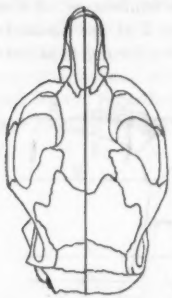


FIG. 12.—Variation of the skull with age in *Microtus m. yosemite:* dorsal aspect. Left half of the skull of adult No. 3835 upon the left, separated by medial line from right half of skull of juvenile No. 3857 upon the right; the condylo-basilar dimension of both magnified to the same size

Although the nasals are of practically the same relative length in the two extremes of age, the rostrum is slightly shorter in juveniles, the brevity of which is further accentuated by the lack at this age of pronounced anterior projection of the incisors. The transverse measurement of the superior portion of the rostrum between the anteorbital fossae may be actually just as great in juveniles, although this apparently is not always the case. Where such proportionately greater breadth exists it still further lends the appearance of shortness to the juvenile rostrum.

Inferiorly, the bullae are relatively slightly larger in juveniles, especially in the width of the anterior portion, but the pterygoid region is considerably shorter in the case of animals of this age. In the two smallest juveniles available the incisive foramina are located relatively farther forward than in adults, which probably means that the anterior growth of the premaxillae, as age advances, is at a greater rate than that of the maxillae.

TABLE III.—*Measurements of the skulls of males (in millimeters)*

Collection number	Condylo-basilar length	Condylo-zygomatic length	Alveolo-basilar length	Condylo-palatal length	Zygomatic width	Interorbital width	Lambdoidal width	Height	Tooth row	Incisive foramina	Alveolar width	Nasals	Angular process
3835	28.2	23.3	16.5	13.4	17.0	3.7	13.0	10.9	7.2	5.6	5.9	8.0	6.2
3837	27.7	23.0	16.3	13.0	17.3	3.8	12.9	11.2	7.0	6.0	5.7	8.8	5.8
3812	27.6	22.9	16.4	13.1	17.9	3.9	13.5	10.9	7.0	5.8	5.9	8.3	6.2
3826	27.5	22.9	16.2	13.3	16.7	3.9	12.9	11.2	7.0	5.6	5.9	8.0	6.3
3853	27.5	22.9	16.3	12.8	16.6	4.1	12.6	10.8	6.8	5.7	5.6	8.6	5.6
3825	27.3	22.8	16.0	13.3	16.8	4.0	12.9	10.8	6.7	5.8	5.7	8.3	5.8
3864	27.3	22.7	15.9	13.0	17.1	3.7	12.5	11.1	6.8	5.6	5.7	8.3	5.9
3822	27.2	22.5	16.1	12.9	16.6	3.7	12.7	10.9	6.9	5.4	5.7	7.7	5.9
3818	27.2	22.5	16.5	13.2	17.0	4.1	12.6	10.8	7.2	5.7	6.1	8.8	5.6
3864	27.1	22.5	16.0	12.8	16.8	3.8	12.9	11.2	6.8	5.8	5.7	8.2	5.5
3846	26.1	21.9	15.6	12.3	16.5	3.8	12.4	10.9	6.7	5.2	5.6	7.8	5.6
3855	25.9	21.6	15.3	12.3	16.2	3.8	12.0	10.8	6.8	5.6	5.7	7.6	5.1
3848	25.9	21.2	15.2	12.1	15.1	3.7	12.1	10.7	6.4	5.7	5.3	7.3	5.2
3862	25.7	21.3	14.8	12.1	15.3	3.6	12.3	10.2	6.7	5.0	5.7	7.5	5.6
3883	25.6	21.7	15.1	12.2	15.5	4.0	12.3	10.6	6.7	5.5	5.5	7.5	5.5
3820	25.6	21.3	15.0	12.2	14.9	3.6	11.7	10.2	6.5	5.5	5.4	7.3	5.2
3841	25.4	21.2	14.7	12.1	15.4	3.9	12.1	10.4	6.5	5.5	5.5	7.0	5.4
3870	25.1	20.9	14.8	11.2	15.6	4.0	12.2	10.8	6.6	5.2	5.5	-----	5.6
3847	24.9	20.7	14.8	12.0	15.2	3.8	12.2	10.5	6.3	5.2	5.3	7.3	5.4
3867	24.7	20.9	14.6	12.3	14.7	3.9	11.9	10.7	6.5	5.3	5.4	6.9	5.5
3887	24.5	20.3	14.3	11.4	14.4	3.6	11.7	10.2	6.1	5.4	5.4	6.9	4.6
3814	24.4	20.5	14.3	11.4	15.0	3.7	11.9	10.2	6.2	5.2	5.4	7.0	4.7
3849	24.3	20.5	14.3	11.2	15.3	3.7	12.1	10.4	6.4	5.2	5.5	7.0	5.0
3801	23.4	19.8	14.2	11.2	14.1	3.5	11.4	9.7	6.2	4.9	5.3	7.0	4.8
3857	22.7	19.3	13.5	10.6	14.4	3.6	11.2	10.1	5.9	4.7	5.2	6.5	4.6
[a] Averages	26.2	21.8	15.45	12.45	16.0	3.84	12.4	10.7	6.68	5.5	5.6	7.74	5.6

[a] Average measurements of 19 (roughly, three-quarters) of the skulls of males, the largest two and smallest four specimens being eliminated from consideration.

TABLE IV.—*Measurements of the skulls of females (in millimeters)*

Collection number	Condylo-basilar length	Condylo-zygomatic length	Alveolo-basilar length	Condylo-palatal length	Zygomatic width	Interorbital width	Lambdoidal width	Height	Tooth row	Incisive foramina	Alveolar width	Nasals	Angular process
3815	27.6	22.9	16.2	12.5	17.0	3.9	12.8	11.1	6.9	5.6	5.7	8.5	5.5
3856	27.4	22.8	16.2	13.0	16.5	3.9	12.8	11.2	6.9	5.5	5.8	8.3	5.2
3865	26.9	22.2	15.9	12.9	16.0	3.6	12.4	10.8	7.1	5.6	5.8	8.2	5.2
3819	26.9	22.2	16.5	12.3	17.1	3.7	12.7	10.9	7.2	5.5	5.9	8.3	5.5
3844	26.8	22.3	15.8	12.3	17.6	3.7	13.1	11.1	7.0	5.7	6.0	8.3	5.7
3871	26.8	22.1	15.3	13.1	15.9	3.7	12.4	10.7	6.7	5.5	5.7	7.6	6.1
3816	26.8	22.0	15.7	12.5	15.9	3.7	12.1	10.6	6.6	5.3	5.6	8.0	6.2
3845	26.8	22.3	16.1	12.0	16.6	3.8	12.6	10.9	7.0	5.3	5.8	8.3	5.6
3817	26.7	21.7	15.5	12.8	15.9	3.6	12.3	10.6	6.6	5.4	5.5	7.9	5.6
3884	26.7	22.0	16.2	12.3	16.4	4.1	12.8	11.0	7.3	5.3	5.6	8.0	5.2
3836	26.7	22.2	15.6	12.7	16.8	3.9	12.2	10.3	7.4	5.2	5.8	7.8	5.7
3881	26.4	21.7	15.9	12.1	16.5	3.9	12.3	10.9	6.9	5.5	5.8	7.7	5.5
3877	26.0	21.3	15.8	12.1	16.1	3.6	12.4	10.5	7.0	5.0	5.9	7.4	5.1
3863	25.8	21.5	16.0	12.1	16.8	4.0	12.3	11.0	7.2	5.5	5.7	7.7	5.5
3869	25.8	21.2	15.1	12.1	15.4	3.8	11.7	10.7	6.4	5.1	5.5	7.7	5.2
3876	25.7	21.2	15.3	12.2	16.6	3.7	12.3	10.6	6.6	5.5	5.7	7.5	5.6
3831	25.7	21.1	15.6	12.1	15.8	3.9	12.3	10.6	6.9	5.4	5.4	7.4	5.6
3821	25.6	21.4	15.2	11.8	15.4	3.9	11.9	10.6	6.5	5.5	5.4	7.4	5.0
3840	25.5	21.2	15.1	11.5	15.2	3.8	11.9	10.5	6.4	5.4	5.6	7.3	5.0
3880	25.5	21.4	15.2	12.5	15.5	4.0	12.0	11.1	6.6	5.5	5.6	7.5	5.4
3830	25.5	21.5	15.0	11.8	15.1	3.8	11.9	10.8	6.5	5.4	5.4	7.4	5.2
3827	25.4	21.7	14.6	12.1	15.9	4.0	12.2	11.0	6.6	5.2	5.5	7.2	5.3
3828	25.4	20.9	15.1	11.8	15.0	3.7	11.9	10.5	6.0	5.3	5.4	7.8	4.7
3872	25.4	21.2	15.0	12.2	15.1	3.7	11.8	10.8	7.4	5.3	5.6	7.5	5.4
3838	25.4	20.9	15.1	12.1	15.0	3.6	11.7	10.8	6.2	5.2	5.4	7.5	4.7
3850	25.2	20.8	14.8	11.7	14.6	3.7	11.6	10.4	6.7	5.3	5.6	7.1	4.7
3885	25.1	20.7	15.2	11.8	15.4	3.9	12.0	10.6	6.9	5.6	5.6	7.0	5.0
3886	25.0	20.7	14.6	11.3	15.1	3.8	11.4	10.9	6.1	5.3	5.6	7.0	5.1
3873	24.9	21.2	14.7	12.2	15.0	3.6	11.2	10.6	6.6	5.0	5.5	7.0	5.2
3813	24.9	21.0	14.8	11.9	14.6	3.6	11.5	10.1	6.8	5.8	5.4	7.4	4.7
3882	24.9	21.2	14.9	11.5	14.8	3.8	11.9	10.5	6.7	5.2	5.4	7.1	4.8
3839	24.9	20.7	14.7	11.3	14.3	3.6	11.4	10.3	6.4	5.4	5.4	7.1	4.7
3853	24.8	20.6	14.7	11.2	15.3	3.8	11.7	10.3	6.4	5.2	5.5	7.3	5.0
3829	24.7	20.5	14.9	11.5	14.7	3.7	11.6	10.2	6.5	5.4	5.4	7.4	4.7
3842	24.6	20.5	14.7	11.4	14.8	3.6	11.4	10.5	6.3	5.1	5.4	6.9	4.9
3861	24.6	20.3	14.6	11.5	15.0	3.6	11.4	10.5	6.4	5.0	5.4	7.2	5.0
3860	24.6	20.3	14.8	11.3	15.2	3.6	11.4	10.6	6.5	5.5	5.3	6.8	5.1
3851	24.5	20.6	14.9	11.7	15.4	3.8	12.0	10.5	6.8	5.1	5.3	7.1	5.0
3888	23.8	19.8	14.5	11.2	14.3	3.7	11.2	10.8	6.6	5.0	5.3	7.1	4.8
3832	23.2	19.5	14.1	11.0	14.0	3.6	11.2	10.0	6.3	4.5	5.2	6.9	4.7
3833	22.3	18.8	13.3	10.2	13.6	3.8	11.2	9.8	6.0	4.1	5.0	6.5	4.5
[a] Averages	25.7	21.34	15.27	12.0	15.63	3.77	11.99	10.65	6.7	5.35	5.5	7.5	5.24

[a] Average measurements of 32 (roughly three-quarters) of the skulls of females, the three largest and six smallest specimens having been eliminated.

In lateral profile the skulls of juveniles are evenly rounded, with a sharper curve barely perceptible at the posterior portion of the frontals and no undue prominence at the anterior margin of these bones. In older animals the dorsal profile is very much less rounded. In the larger subadults the greatest prominence has shifted to the vicinity of the nasal-frontal suture, while in adults this has increased, with considerable angularity and pronounced declivity of the rostrum in many cases. There is individual variation of limited extent in this outline and in the exact age at which the change is apparent. In transverse outline from a posterior view the braincase in juveniles is proportionately higher and therefore narrower, and more evenly arched, or in other words, more nearly circular; while in the case of adults this outline is much more oval.

COMPOSITE MEASUREMENTS

The composite measurements have been as follows:

CONDYLO-BASILAR LENGTH.—The average of this measurement for the 19 intermediate males (see footnote, Table III, p. 996) is 26.2 mm., with extremes

of 27.6 and 24.5, a difference of 3.1 mm., or 11.8 per cent of the average. For females the average is 25.7 mm., with extremes of 26.9 and 24.6, a difference of 2.3 mm., or only 8.9 per cent. These figures, as well as subsequent ones, are a further indication of the fact that males exhibit greater extremes of development with less conservatism of characters than do females.

CONDYLO-ZYGOMATIC LENGTH.—From the condyle to the antero-superior edge of the zygomatic process of the maxilla. The tables give an average of 21.8 for males, with extremes of 22.9 and 20.3, a difference of 2.6 mm., or 11.9 per cent of the average. The average for females is 21.34, with extremes of 22.3 and 20.5, a difference of 1.8 mm., or 8.4 per cent. This is an excellent measurement, dependable, with little individual variation, and is correlated closely with condylo-basilar length. The latter measurement, however, is preferable, and in cases where it is taken, as it should be, it is of value when used with the condylo-basilar measurement as an index to the development of the rostrum.

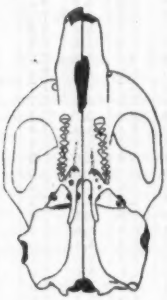


FIG. 13.—Variation of the skull with age in *Microtus m. yosemite:* ventral aspect. Left half of the skull of adult No. 3855, upon the left, separated by medial line from right half of skull of juvenal No. 3857, upon the right: condylo-basilar dimensions of both magnified to the same size

ALVEOLO-BASILAR LENGTH.—The distance from the posterior end of the last molar to the posterior edge of the incisive alveolus. For males the average of this measurement is 15.45 mm., with extremes of 16.5 and 14.3, a difference of 2.2 mm., or 14.2 per cent of the average. For females the average is 15.27 mm., with extremes of 16.5 and 14.6, a difference of 1.9 mm., or 12.4 per cent. This is a rather good measurement, as it seems to be of considerable importance in general diagnostic work among microtines. Its variation is not excessive with age nor individually, and it is preferable to the measurement of the diastema, to which it is somewhat similar, for the latter must be measured with greater care in order to prove accurate.

CONDYLO-PALATAL LENGTH.—This measurement is from the condyle to the anterior point of the bony shelf of the palate. The average for this measurement in males is 12.45 mm., with extremes of 13.3 and 11.2, a difference of 2.1 mm., or 16.8 per cent. For females the average is 12 mm., with extremes of 13.1 and 11.2, a difference of 1.9 mm., or 15.8 per cent. This measurement varies to a considerable extent individually and more with age, but it is probably the most valuable measurement to use in precise work as an index to the development of this portion of the skull. The chief and probably the only objection to its use is the fact that while taking it the delicate processes often present upon the bony shelf of the palate, which may be of the greatest importance in specific or group diagnoses, are extremely subject to injury.

HEIGHT OF SKULL.—The perpendicular distance from a plane passing from the most inferior point of the bulla along the crown of the most prominent molar to the highest point of the cranium. The average of this measurement for males is 10.72 mm., with extremes of 11.2 and 10.2, a difference of 1 mm., or 9.3 per cent. For females the average is 10.65 mm., with extremes of 11.1 and 10.1, again a difference of 1 mm., or 9.4 per cent. The height of the cranium is an extremely useful measurement to take, especially when it is used in comparative work with the condylo-basilar length as an index. Another character that is valuable in the case of microtines is the angle formed by the molar row with the plane passing from the bullae to the most prominent molars. In many

other families and subfamilies, however, height of the cranium can not satisfactorily be taken in just this manner, but special methods must be devised, as height from the pterygoid plates, or measured from the alveolar border between the penultimate and last molars. A scrutiny of the series at hand shows that the actual height of the posterior portion of the braincase differs hardly at all

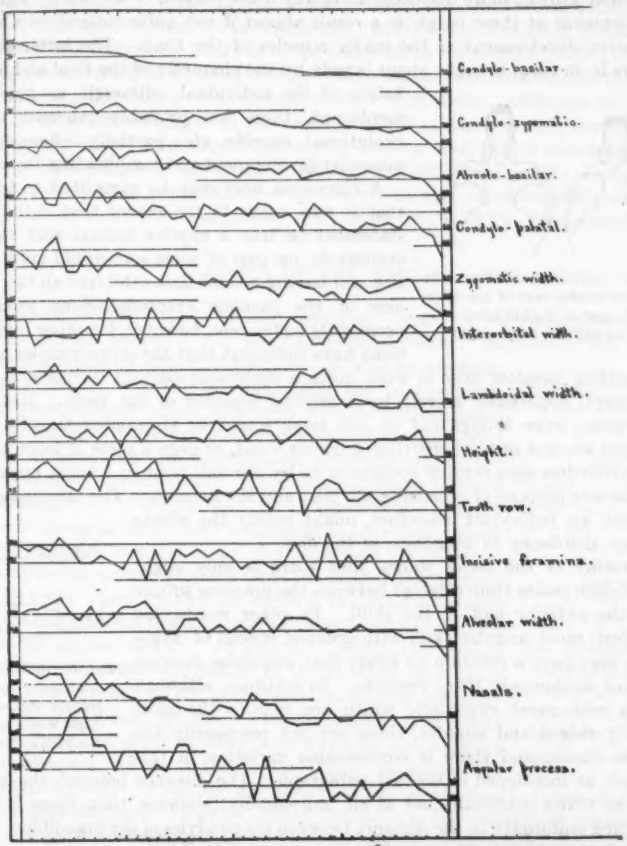


FIG. 14.—Graph for skull measurements of the female series, reduced to percentages, with the largest skull considered as par, and arranged according to condylo-basilar sequence

with age, although there is some individual variation in this measurement. The difference with age shown in the tables is caused chiefly by variation in the infero-superior dimension of the bullae, but the height measured from the inferior border of the foramen magnum is almost uniform. Unfortunately, without calipers of special design it is practically impossible to measure the height of skull after this fashion with a satisfactory degree of uniformity.

ZYGOMATIC WIDTH.—The greatest spread of the zygomatic arches. The average of this measurement for males is 16 mm., with extremes of 17.9 and 14.4, giving a variation of 3.5 mm., or 21.9 per cent. For females the average is 15.63 mm., with extremes of 17.6 and 14.6, a difference of 3 mm., or 19.2 per cent.

As can be seen, the variation, both individual and with age, of this measurement is great, and the variability in the exact configuration of the zygomata is even greater.

The development of the zygomatic region is considerably involved, and this, together with the temporal and lambdoidal ridges, reflects the influences of the muscular growth more decidedly than any other portion of the skull. Excessive development at these points is a result almost if not quite entirely of a similar excessive development of the major muscles of the head. The latter state of affairs is, in turn, brought about largely by the character of the food and feeding habits of the individual, although, as previously mentioned, there are probably inherent trends, evolutional, specific, etc., partially influencing the muscular development and complicating the results.

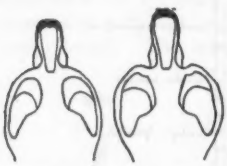


FIG. 15.—Individual variation in the lateral development of the zygomatic arches of adult mice. No. 3848 on left; No. 3864 on right

A digression here may be permitted to indicate that it may occur to the reader that if the above statement be true a captive animal that was fed exclusively on pap of some sort would grow to full size still having a skull that exhibited all the weakness of the juvenile cranium. Such would not necessarily be the case, however, for other investigations have indicated that the unworn molar pattern of nestling meadow mice is worn down a surprising amount during a space of two days, apparently merely by a gritting together of the teeth. Hence an individual, even though fed on soft food, might be stimulated thereby to an unusual amount of teeth-gritting, gnawing wood, or even a piece of loose wire, as the writer has seen captive specimens do by the half hour at a time, apparently for the sole purpose of exercising the jaws and the muscles. The inherent desires of such an individual, therefore, might nullify the effects of any deficiency in toughness of the diet.

FIG. 16.—Individual variation in depth of the zygomatic arch of adults. Right lateral aspects of No. 3835, *a*; No. 3845, *b*

Scrutiny of the series shows that there is only slight correlation (aside from ridging) between the cranium proper and the anterior half of the skull. In other words, the squarest, most angular skull with greatest spread of zygomata may have a cranium no larger than examples showing marked weakness in these respects. In addition, although skulls with great zygomatic width are usually the most heavily ridged and angular, these are not necessarily the largest skulls, and there is considerable variation in this respect, as mentioned in the last paragraph. The distance between the glenoid cavities varies practically not at all individually, showing that there is corresponding uniformity in the distance between the condyles of the mandible. There is much variation in the degree of lateral projection of the zygomatic processes of the squamosals, this conforming to the amount of angularity exhibited by the remainder of the zygomata. It is in the region of the zygomatic processes of the maxillae, from which arise the masseter muscles, that any difference in the strength and angularity of the skull is most pronounced, for it is there that variation in the development of this great muscle is directly manifested.

In specimens showing the greatest angularity and width of the zygomata the septum formed by the maxillary root is correspondingly extensive, the antero-superior indentation more accentuated, and the superior border often heavier. As the process extends from the long axis of the skull at more nearly a right angle, the anterior angle of the zygomatic arch is better defined in the examples with greatest zygomatic width. Correlated with the above points is corresponding angularity of the lower jaw, as discussed under the proper heading.

Measurements of height of the rostrum are not here presented for the reason that it is impossible to obtain them with any sort of uniformity. This, nevertheless, is a character of great importance in specific diagnosis. Individual variation is great, especially in the height of the posterior portion of the rostrum. Maximum height, or depth, of this member is practically always accompanied by pronounced declivity of the supero-lateral profile. In other words, great depth of the skull is accentuated in this region and but little or not at all in the anterior portion of the rostrum. There is equal variation in its ventral profile; in some this is almost straight, while in others, chiefly those with considerable depth of this member, it exhibits pronounced concave curvature. Although as a rule there is no great difference in the relative length of the rostrum, several individuals have rostra that are conspicuously stubby, and this is correlated only partially with length of the nasals. Female No. 3827 is especially noteworthy in this respect, as an examination of its condylo-basilar, condylo-zygomatic, and nasal measurements, in comparison with those of No. 3876, for instance, will show.

BONES OF THE SKULL

OCCIPITAL.—This bone is divided into three areas, the supraoccipital above, the exoccipitals laterally, and the basioccipital below. Superiorly the supraoccipital articulates with the interparietal and squamosals; the exoccipitals with the mastoids; and the basioccipital, skirting the auditory bullae, anteriorly with the basisphenoid. To the occipital bone are attached many of the powerful cervical muscles, and its configuration therefore reflects the degree of their development. A pronounced tilting forward of the occipital is acknowledged to be a modification brought about by fossorial habits and is supposed to have been caused by the stresses brought upon the bone and its attached muscles by the animal pushing aside the earth of the burrows with its head. Incidentally, the writer is not at all convinced that other life habits besides fossorial ones do not bring about somewhat similar results. At any rate, within the present series there is excessive variation in the forward inclination and all other aspects of the occipital when viewed vertically from above. In fact, hardly any two examples are precisely alike in the shape of the superior border and the irregularities of the posterior surface of this bone. These variations are present irrespective of age and are purely individual, the result of variation in the cervical musculature. There is similar variation in the visibility of the condyles when the skull is viewed from above; in some specimens they can not be seen, in a few they are prominent, but in the majority they are barely perceptible. This difference, largely individual, is usually caused by the configuration of the supraoccipital, but is also due to the fact that in the younger animals the condyles are shorter. There is like difference in the exact shape and size of the foramen magnum, irrespective of age.

FIG. 17.—Individual variation in depth of rostrum and declivity of its dorsal outline in adult skulls. No. 3865 above; No. 3826 below

The superior borders of the lambdoidal processes of the occipital form the posterior faces of the lambdoidal crests. The degree to which these are developed depends upon the strength of the temporal muscles which are attached to them, and therefore their prominence is also correlated with the temporal ridges and to only a slightly lesser degree with the angularity and strength of the whole skull. There are lambdoidal crests of respectable size, however, in

animals that are barely matured, and upon which there is not as yet pronounced temporal ridging, and the variation is never so decided and abrupt as in the latter character. In juveniles the lambdoidal crests are inconspicuous.

There is some slight variation of the exoccipitals, and in young animals the sutures between these and the mastoids are relatively unraised. There is much variation, however, in the development of the paroccipital processes. In all but the smallest juveniles there is little age variation, but in these, although the processes are of respectable length, they closely embrace the bullae and are consequently directed slightly forward of the perpendicular. In adults and subadults they are, as a rule, only slightly longer proportionately, but the distal extremities are usually free from the bullae and are directed slightly rearward of the perpendicular. The variation is chiefly in the length and the degree of the infero-medial curvature of the tips, which in most of the specimens is moderate. The sole function of these processes seems to be for the attachment of the digastric muscles. This being the case, it appears that these processes are somewhat better developed in juveniles than the condition of the general musculature of the head at this age might lead us to expect, pointing to the probability that the digastric may be of more than ordinary importance in the economy of these mammals. In juveniles the margins of the basioccipital closely embrace the audital bullae, but in older examples there are vacuities at the lateral margins, these depending upon variation in the width of a slight constriction of the bone directly posterior to the basioccipital-sphenoid suture.

INTERPARIETAL.—This bone articulates anteriorly with the parietals, laterally to a varying extent with the squamosals, and posteriorly with the supraoccipital. It is highly variable in shape not because of any muscular attachments, but for the reason that its position renders it particularly subject to distortion by the development of adjoining parts of the cranium. The antero-posterior dimension varies from about 3.1 to 3.7 mm., and the transverse one from 6.1 in a very old individual to 8 mm. In the majority of individuals this bone is almost exactly twice as long as wide. There seems to be very little variation from juvenility to middle life. In the largest adults, however, the relative, and even actual, decrease in the prelambdoidal width of the braincase, with consequent narrowing of the distance between the temporal ridges, makes this bone *appear* narrower. In addition, the fact that it *is* narrower in some of these examples can not be ignored. This state of affairs may be attributable to strains imposed upon it by a greater growth force in the development and encroachment of the squamosals, with consequent absorption of the lateral margins of the interparietal, an explanation that is entirely logical if this really be the weaker bone, as seems to be the case.

Variation in the precise form of the anterior outline of the interparietal is almost infinite. In a few specimens this follows the form of a gentle, convex arc. In many others an almost straight line is broken by a rather sharp projection of the medial portion into a point. In the majority the sutures with the parietals follow a very wide obtuse angle, while in a number of others this angle is somewhat sharper and less obtuse. There is such variation, however, that it is not practicable to divide the series into definite groups based upon this character.

The suture with the squamosal may form almost a right angle with that with the occipital, but in the majority of cases the angle is of about 30° to 35° (the apex directed laterally). In still others the angle is considerably sharper, due to a greater prolongation of its apex. (See lower detail, fig. 18.) In almost all cases this suture pursues a very erratic course. That with the supraoccipital is usually practically straight or very gently curved. A slight, very obtuse

angle is sometimes formed, however, or an illy defined double curve. There is no definite variation with age.

PARIETALS.—Anteriorly this pair of bones articulates with the frontals, laterally with the squamosals, and posteriorly with the interparietal. Antero-medially there is a recession of the parietals, filled by a part of the frontals, and each has an anterior projection and a lateral one. These projections and recessions are least developed in juveniles, but after the attainment of sexual maturity there is negligible variation with age, though much individually. This is more pronounced in the anterior than in the posterior projection, though there are a few exceptions to this rule.

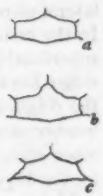


FIG. 18.—Individual variation of the interparietal in the skulls of adults. *a*, No. 3817; *b*, No. 3815; *c*, No. 3836

The temporal ridges are continuations, almost at right angles, of the lambdoidal crests. From the latter they cross the extreme lateral borders of the interparietal, extend across the bases of the lateral projections of the parietals, and almost always follow the borders of the anterior ones to their antero-medial tips, thence joining the interorbital ridging. Occasionally, however, the temporal ridges cut across a part of the anterior projections. Differences in their precise positions depend almost altogether upon similar differences in the shape of the parietals. The degree to which these ridges are developed is dependent upon the development of the temporal muscles. Therefore the strongest, most angular skulls have the best-defined temporal ridges, while in weaker, rounded skulls with narrow zygomatic width they are poorly defined. They may be lacking or quite distinct in medium-sized subadults, but in individuals which are fully adult they are always apparent, though in varying degree. On the whole, this character is perhaps better defined in males, although there are female skulls that are fully as heavily ridged.

SQUAMOSALS.—Each squamosal articulates posteriorly with the occipital and mastoid, medially to a slight extent with the interparietal as well as with the parietal, anteriorly with the frontal, and laterally with the alisphenoid and mastoid. The jugal articulates with the zygomatic root of the squamosal. Perhaps the chief variation in the outline of this bone lies contiguous to the anterior projection of the parietal. In some individuals, especially the youngest ones, the squamoso-frontal suture begins at a point upon the antero-lateral margin of this projection, while in the majority it is situated relatively more medial. It is also influenced by the size of the anterior projection of the parietal. The squamosal-interparietal suture differs individually, but not with age, in extent and exact shape as pointed out in the discussion of the interparietal. The posterior border of the squamosal constitutes the anterior face of the lambdoidal crest and immediately anterior to this is situated the prelambdoidal fenestrum of the squamosal. This is not a true foramen in the bone, but rather seems to have been formed in remote times by an invagination of the bone from its posterior border, the posterior edges of the fenestrum having joined at a later period, the resulting false suture being plainly distinguishable in juveniles but disappearing with age in this species, although it is not so lost in some other genera of this subfamily. The exact size of this fenestrum is highly variable individually, in length about 20 per cent. Its infero-lateral border is formed of a slender bar of bone, and infero-laterally to this is the premastoid vacuity, usually well defined but occasionally practically obliterated.

FIG. 19.—Individual variation of the parietals in adult skulls. *a*, No. 3815; *b*, No. 3863; *c*, No. 3864

There is much variation in the precise angle and the amount of projection of the zygomatic root of this bone. The greatest degree is, of course, met with in the case of individuals with maximum zygomatic width, and in these the angle is less acute. As previously mentioned, the zygomatic width is greatest in skulls that are most heavily ridged, and in such the postorbital processes of the squamosals are also somewhat better developed and more angular, the prominence of the latter depending directly upon the development of the deep portion of the temporal muscle. In animals with greatest development of this character the lateral slope of the anterior border of the braincase is most abrupt and squarish. In the case of heavily ridged and angular skulls the pull exerted by the powerful superficial part of the temporal muscles from their attachments upon the temporal ridges has actually flattened out the underlying portion of the squamosals between the ridges and the zygomatic processes, making them flatter than is the case in weaker skulls. Thus the temporal ridges, instead of being true ridges such as often occur in the interorbital region, are in reality the apices of angles formed by the superior and lateral surfaces of the cranium.

MASTOIDS.—The mastoid is very irregular in outline and closely embraces the audital bulla supero-medially. In the articulated skull it occupies the space on either side between the lambdoidal process, being bounded supero-medially by the exoccipital. The anterior portion, embracing the audital bulla, is visible within the prelambdoidal fenestrum and along the premastoid vacuity. The visible portion is quite variable, depending directly, upon analogous differences in the adjoining border of the occipital.

AUDITAL BULLAE.—Each one of these globular bones seems to form a true suture only with the mastoid, although there are false sutures connecting it more or less securely with the basi- and alisphenoids, squamosal, and basioccipital. Variation in the audital bulla is not of such a nature as to be measured readily, and one should be cautious in making statements regarding variations of an intangible sort. There is slight variation with age, the greatest being in the width of the anterior portion, and the whole being perhaps more globular in juveniles. There is little individual, proportionate variation, although a few specimens do have bullae that are slightly more globular than the average. It is in the relative size, or mass, that the chief difference lies. Upon the whole, this is of a sufficient amount so that it must be taken into consideration, but is not excessive. The auditory meatus varies but slightly in shape and size. In adult skulls, however, the antero-superior border projects laterally to a considerably greater extent than is the case with juveniles.

SPHENOIDS.—The articulations between the sphenoid bones are not always to be distinguished without difficulty in skulls of such small size. The alisphenoid articulates with the squamosal, frontal, maxilla, and the other sphenoids. Superiorly the suture formed by its connection with the squamosal extends forward from a point barely inferior to the premastoid vacuity to its junction with the frontal at a point slightly antero-medial to the postorbital process; thence it descends along the frontal to the orbitosphenoid and the sphenoidal fissure. From the latter the maxillary-alisphenoid suture extends obliquely rearward to join the external pterygoid plate immediately posterior to the third molar. The alisphenoid constitutes the entire lateral surface of this plate and the posterior portion of its medial surface, as well as the posterior portion of the floor of the pterygoid fossa. Although there are, of course, many differences in the precise configuration of this bone, these are relatively slight in degree. The most apparent difference occurs in animals of the two extremes of age through the lengthening of the pterygoid region as the animal grows, with consequent

elongation of the external pterygoids to form an angle with the axis of the skull of increasing acuteness, this in response to the development of the pterygoid muscles, chiefly the internal ones. It should be noted that there occurs a minimum of variation in the size and depth of the pterygoid fossae, except with age as noted.

Between the maxilla, orbitosphenoids, and alisphenoids occurs the large sphenoidal fissure, through which pass several important nerves and blood vessels. Directly supero-lateral to the external pterygoid plate are situated the foramen rotundum and foramen ovale, the latter being the posterior one and by far the larger. In this, however, as in many other species, the foramen rotundum varies much in size, and in a few cases is virtually blended with its neighbor.

BASISPHENOID.—This bone articulates posteriorly with the basioccipital and anteriorly with the presphenoid. It then descends antero-inferiorly, articulating with the palatines to form all but the anterior base of the internal pterygoid plates. The numerous foramina and vacuities in the pterygoid region are large and extensive in the present species. Especially worthy of note is the vacuity in the anterior portion of either internal pterygoid plate and those on either side of the presphenoid. At times these will be found to be of aid in diagnosis. On the whole, these vacuities are rather constant individually, but they are proportionately very much smaller in younger animals. The internal pterygoid plates not only appear to be relatively heavier in juveniles because shorter, but they are actually heavier (wider) in inferior aspect than in the majority of older examples. There is also considerable individual variation not only in the apparent thickness of these plates, but in the shape. In some cases the two are practically parallel, in the majority they diverge slightly, while in the case of a few there is a marked tendency for the posterior halves to flare.

FIG. 20.—Individual variation in the palatal shelf and internal pterygoid plates of the adult skull. *a*, No. 3812; *b*, No. 3845; *c*, No. 3837; *d*, No. 3829

PRESPHENOID.—In the present species, as in many, if not most, microtines, the juncture of the basisphenoids and presphenoids can not be distinguished with certainty, even in juveniles. It can be described in the genus Ondatra, however, and from analogy with that it is possible to state with a degree of certainty that this bone begins at a point slightly posterior to the posterior vacuities upon the floor (or rather roof) of the interpterygoid fossa. It thence extends anteriorly, in the form of a rod, to join the vomer. The slender bridges of bone joining it upon either side are the presphenoid processes of the basisphenoid.

ORBITOSPHENOIDS.—Externally the orbitosphenoid is of little consequence in the present species. It appears as a very small bone forming the anteromedial wall of the sphenoidal fissure and is pierced by the optic foramen. It articulates with the alisphenoid, maxilla, and frontal.

PALATALS.—The suture between the paired palatals can be distinguished only in the youngest juveniles at hand. Each of these bones constitutes the extreme anterior portion of the internal pterygoid plate, the anterior part of the pterygoid fossa, the anterior half of the medial face of the external pterygoid plate, and together, the palatal shelf. The palato-maxillary suture lies parallel and just medial to the molar alveoli, and the anterior border of the bone is situated at a point lying between the middles of the second molars. Important details to be considered are the shelf of the palate and the palatal pits. There is much variation in the width and shape of the former, this being of a nature impossible

to classify with precision. In the majority of individuals the shelf is squarish in general outline, there being a slight medial notch flanked upon either side by a minute process, often spinous. These processes, however, are sometimes lacking, and the notch varies in size, at times being entirely absent, so that the shelf is then practically unbroken in outline. In a few examples the entire anterior portion of the interpterygoid fossa gradually tapers to a point. This variation is not dependent upon age but is entirely individual. The lateral shelves of the palatines (antero-lateral to the fossa) are also quite variable in exact configuration, probably being largely influenced by the development of the internal pterygoid muscles. The depth of the palatal pits also varies individually to a great extent, though not relatively with age. Finally, the entire palatal bone is pierced by many minute foramina and studded with tiny pits, no two being precisely alike in this respect. Hence, it is seen that individual variation in the palatal region is so great and of so intangible a nature (the several types being so inextricably blended) that these characters can be used only after careful deliberation.

FRONTALS.—The suture between these paired bones is clearly distinguishable in juveniles, but has disappeared by the time that the animal has attained sexual maturity. Each frontal articulates with the parietal, squamosal, alisphenoid, maxilla, premaxilla, lachrymal, and nasal. The posterior portion is characterized by great individual variation caused chiefly by the position of the squamosofrontal suture. The posterior point of this may be either lateral or medial to the margin of the interorbital constriction; or in other words, it may be situated at either the lateral or medial edge of the anterior projection of the parietal. Most of the other sutures vary but slightly, and there are no age differences save that in juveniles the irregularities of the bone are more poorly defined and less abrupt. There are some individual differences anteriorly, but these are discussed elsewhere.

The chief interest in this pair of bones lies in the interorbital region. The only variation in the width of this, measured at its narrowest portion, is individual. Not only is it actually just as great in young animals, but may be greater, while among the examples with narrowest interorbital are some of the largest adults. In normal males this averages 3.84 mm., with extremes of 4.1 and 3.6, a difference of 0.5 mm., or 13 per cent. In females, the average is 3.77 mm., also with extremes of 4.1 and 3.6, a difference of 13.3 per cent of the average.

Normally there are two interorbital ridges, these being in reality anterior extensions of the temporal ridges and terminating at the postero-lateral edges of the nasals. They are absent in the smallest juveniles, though definable in large juveniles and practically all older individuals. In a very few, however, they are to all intents absent. There is great variation in the degree of definition in these ridges, as well as in the distance between them and all other details. There is a tendency for them to coalesce with advancing age, with consequent elimination of the intervening sulcus. Most, but not all, of the largest adults thus have single interorbital crests. Similarly, the sulcus is quite wide in many of the smaller subadults, though narrower in the majority, while it is well-nigh obliterated in a few, even of those that are barely sexually mature. The writer is led to believe that in those large adults now having a sulcus the latter was of unusual width in their youth, and vice versa. Animals with a tendency toward coalescence of the ridges usually show indications of a strong, angular braincase. But, on the other hand, this is not the case in the individuals of such a large minority that one hesitates at reaching any definite decision as to cause. Males are somewhat more heavily ridged in this region than are females.

The anterior portion of the braincase, and therefore the posterior portion of the interorbital, is amenable to the effects of the anterior part of the temporal muscles. No important muscles of mastication arise from the anterior portion of the interorbital, such as would logically develop a crest or ridges, and other causes are therefore responsible for their formation. Explanatory theories may be suggested for the growth of such, but these can not be proved.

LACHRYMALS.—It was not discovered until after all skulls had been cleaned that in their preparation by means of a fine stream of water, the lachrymals had become loosened and washed away from all but a very few. This bone, however, evidently varies to only a slight extent. When the skull is viewed from above, the lachrymal is seen as a small bone upon the antero-supero-medial border of the orbit. It embraces a small portion of the frontal and then extends along the zygomatic root of the maxilla to slightly lateral of the small lachrymal process of this bone. There is also a thin plate extending anteriorly along the supero-medial face of the anteorbital foramen quite to the anterior opening.

JUGALS.—The jugal or malar articulates posteriorly with the corresponding process of the maxilla. There is some variation in this bone, such depending upon differences in the zygoma as a whole. The posterior suture is strong, the jugal fitting into an indentation in the process of the squamosal, dovetail fashion. The anterior suture is discussed under the next heading.

MAXILLAE.—Each of the two maxillae articulates with the frontal, premaxilla, lachrymal, jugal, orbitosphenoid, alisphenoid, and the palatine. The suture with the frontal occurs at the superior base of the zygomatic process, this uniting with the maxillo-premaxillary suture, which descends to join the incisive foramen at a point slightly anterior to its center. The junction between the two maxillae, extending from these foramina posteriorly to the palatines, is obliterated, even in the youngest animals at hand. Skirting the lateral edge of the palatine, the entire maxillary molar series on either side is included within the maxilla, which then extends from just posterior to the third molar antero-superiorly to the sphenoidal fissure. Thence the frontal-maxillary suture ascends anteriorly to about the center of the anteorbital foramen.

The suture with the frontal at the superior base of the zygomatic process is usually practically parallel with the axis of the skull, but it may slope antero-medially at a considerable angle in some cases. There is practically no variation in the remaining sutures. As previously indicated, there is great variation in the development of the zygomatic process of the maxilla. In juveniles this is weak, and it may be almost as lacking in strength proportionately in subadults. Robustness in this detail is correlated with strength in other portions of the skull and is the result of stimulation by masseter muscles that are stronger than the average. There is little difference, save in the degree of lateral spread, between an angular and a weak skull when viewed from in front. When examined from above, the zygomatic processes of the former will be seen to project from the skull more nearly at right angles. The slight indentation in the bone immediately antero-superior to the anteorbital foramen is always well defined in angular skulls, which may or may not be the case in weaker ones. The slight, spinous process upon the supero-postero-medial border of the root—the lachrymal process—is even more irregular, its precise development, or absence, depending upon the adjoining lachrymal. The exact position of the anteriormost point of the maxillary-jugal suture is quite variable. In some specimens it is situated about even with the anterior face of the first molar, but in the majority it is about one millimeter, and in a few a trifle more to the rearward. The jugal is slightly dovetailed into the maxilla, and the suture extends posteriorly

to within a couple of millimeters of the posterior angle of the zygoma. There is great variation in the supero-inferior aspect of the portion of the maxilla immediately anterior to the jugal. In some (as the largest male) this detail is shallow, while in others (as female No. 3845) it is nearly 50 per cent deeper (see fig. 16), due to the formation of a sharp sort of superior crest. This extreme development is not necessarily present in the most angular skulls, but may develop independently, and is probably in response to certain special stimulation by the deep part of the masseter major muscle, and possibly by the masseter zygomatica as well. The superior border of the root, differing in thickness, is amenable to similar influences by different portions of the masseter.

The anteorbital foramina are about three times as high as wide; but this means little, as it is impossible to measure them with accuracy. They do not vary appreciably except in the antero-posterior extent of the adjoining fossae upon the rostrum. Such differences are dependent upon the development of the anteorbital slip of the deep part of the masseter major. Width of rostrum is usually measured across the prominences anterior to the anteorbital fossae, but these are often fragile and easily injured, and it is an unreliable measurement on which to place dependence.

The shape of the incisive foramina is usually constant in the present series. These are not wide, and there is gradual and moderate, though definite, constriction posteriorly. In the case of normal adults and subadults, the length of the incisive foramina for males averages 5.5 mm., with extremes of 5.8 and 5, a difference of 0.8 mm., or 14.5 per cent of the average. Females average 5.35 mm., with extremes of 5.7 and 5, a difference of 0.7 mm., or 13 per cent. These foramina may be proportionately a trifle shorter and are situated relatively farther forward in juveniles, but after sexual maturity has been attained they vary hardly at all in comparison with the size of the entire skull. There are some examples in which the length of the foramina varies individually to some extent, but on the whole this measurement is quite uniform and dependable.

Premaxillae.—Each of these bones articulates with the nasal, frontal, and maxilla. The ascending branch of the premaxilla projects posteriorly between the nasal and maxilla to join the frontal, and the resulting suture is somewhat variable, but not nearly to the extent that is sometimes to be found in other species. These branches are always pointed at the medial tips and differ negligibly in shape. Variation in the position of the posterior terminations with reference to the posterior terminations of the nasals is considerable, however. In 48 examples the ascending branches extend slightly farther backward while in 16 these may be considered as ending even with the nasals. It may or may not be fortuitous that among the latter large females are especially prevalent.

Nasals.—The nasals are quite variable, probably not from any inherent tendency to vary, but rather because of differences in the stresses brought to bear by surrounding bones. They articulate laterally with the premaxillae and posteriorly with the frontals. The measurement of length of nasals must be taken with extreme care in order to prove reliable. Not only is it sometimes difficult to decide upon the exact posterior terminations, but the anterior tips are exceedingly subject to injury. There is considerable individual variation in length of nasals and also much difference with age, these bones often being relatively shorter (and wider) in juveniles. In males the normal average of this measurement is 7.7 mm., with extremes of 8.8 and 6.9, a difference of 1.9 mm., or 24.7 per cent of the average. For females the average is 7.5 mm., with extremes of 8.3 and 6.9, a difference of 1.4 mm., or 18.6 per cent.

The posterior terminations of the nasals usually present a gently rounded aspect, although in a few they are more squarish, slightly emarginate, or so narrow

as to be almost pointed. It is in width, however, that this portion of the nasals chiefly varies, this difference in extremes amounting to fully 100 per cent. There is normally a slight lateral constriction at about the center of these bones, this being more pronounced in a few and absent in several others. The degree to which the anterior terminations of the nasals are arched, from an anterior aspect, is best shown by an examination of the anterior nares. Their outline varies greatly. In some extremes the height, measured from the nasal-premaxillary suture, is fully half the width of the opening, while at the other extreme are animals with nasals excessively flattened in which the height may be considered as being negligible. This latter type occurs in skulls having wide rostra, and a highly arched condition of the nares is undoubtedly caused by a medial crowding of the premaxillae in early life, due to some obscure stimulus. The degree to which the nasals project anteriorly also varies considerably, but in no case do those of adults hide the incisive processes of the premaxillae when the skull is viewed from above. In juveniles, however, in which the incisors are smaller and project to a lesser degree, the latter are barely visible from above.

MANDIBLE

It was found that there is considerable variation in mandibular characters. The length over all from the condyle to tip of the incisor varies, of course, precisely as does the glenoid cavity to incisor measurement of the skull. The posterior portion of the mandible is essentially a system of levers and scaffolding for muscular insertions to even a greater extent than is the skull; hence its characters are exceedingly sensitive to differences in the variations of the muscles. These mandibular variations, however, are delicate rather than gross, and are of a sort difficult to express by measurements. The coronoid process varies in length, in width (antero-posteriorly), and in the degree to which it slopes rearward, and the same statements apply to the condyle, although variation in the latter is not correlated with that of the coronoid. There is great difference, irrespective of age, in the prominence of the slight process formed by the pulp capsule of the incisor (the incisive process of the condyle). In some examples this is obscure, while in others it is well developed. Its prominence is influenced partially, but not entirely, by the degree to which the condyle is bent inward, that is, out of plane with the remainder of the ramus. This, as well as the angle at which the whole supero-posterior portion of the ramus projects outward from the supero-inferior plane of the molars, varies in degree with the zygomatic width of the skull. The widest skulls usually, if not always, are accompanied by the most angular mandibles, often with prominent eminences at the roots of the incisors. The angular process, as well, usually follows such a trend. Its length, however, and its supero-inferior width vary independently of the other two processes, development being influenced by different muscles. The length of the angular process, measured from the prominence formed by the root of the posterior molar to its tip, is given in the tables; but neither this measurement nor that of any other portion of the mandible is deemed of great significance in systematic work with microtines when the accompanying skull is available.

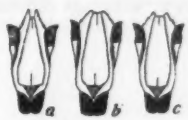


FIG. 21.—Individual variation of the nasals and ascending branches of the premaxillae in adult skulls. *a*, No. 3830; *b*, No. 3836; *c*, No. 3871

The masseteric ridge does not vary individually to an appreciable extent and only very slightly with age. The coronoid process and the condyle are proportionately large in juveniles, but the angular process is relatively small. It has not been possible to correlate any of these variations save to the extent mentioned. Variation in the length of the teeth from one cause or another would have a corresponding effect upon the muscles of mastication and their insertions, but it is not known with any degree of certainty just what these are.

THE TEETH

The changes that occur in the teeth of microtines soon after birth are exceedingly interesting and significant. As there are no newly born young in the present series, however, and data on dentition of this group are being presented in another paper under preparation by the author, this subject will not be treated in the present contribution.

Certain teeth, notably the last upper and first lower molars, are exceedingly variable, as is the rule in this subfamily. The tooth pattern of microtines is, of course, of very great value in diagnosing groups and many of the species. In spite of the efforts of many investigators, however, it has proved impossible to correlate minor variations either with age or any other character, and it is strongly felt that an undue importance has often, if not usually, been attached to such differences in enamel pattern in the study of closely related forms. There has been the same failure in the present study, and in spite of the author's best efforts along this line it has not been possible to assign to these variations within the series any significance whatsoever, save that they undoubtedly indicate some active, composite, evolutional trends on the part of the teeth concerned.

There is considerable individual variation in the length of the maxillary tooth row, with age difference to correspond. The average length for males is 6.68

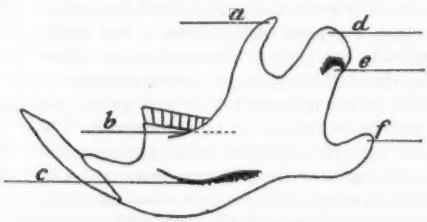


FIG. 22.—Diagrammatic lateral aspect of left ramus of the mandible of adult skull. *a*, Coronoid process; *b*, temporal fossa; *c*, masseteric ridge; *d*, condyle; *e*, incisive process; *f*, angular process

mm., with extremes of 7.2 and 6.1, a difference of 1.1 mm., or 16.4 per cent of the average. The average for females is 6.7 mm., with extremes of 7.4 and 6, a difference of 1.4 mm., or 20.9 per cent. The sexual difference in size in favor of the females, although possibly of some significance, is not sufficiently pronounced to be of much value. It is worthy of note, however, that the greater variation in this character occurs among the females instead of among males, as is usual in the case of most measurements. The size of the alveoli increases with general growth of the skull; hence the individual teeth are broader in both the antero-posterior and lateral dimensions in adults. The alveolar width, greatest distance between the lateral borders of the tooth rows, shows less individual variation, but almost as much variation with age as the length of tooth row. To a slight extent only is it correlated with the latter. In males it averages 5.61 mm., with extremes of 6.1 and 5.3, a difference of 8 mm., or 14.3 per cent. In females it averages 5.52 mm., with extremes of 6 and 5.4, a difference of 0.6 mm., or 10.8 per cent. In this character the greater size, as well as variation, occurs among males.

Variation in molar pattern is not by any means always bilaterally symmetrical, although corresponding teeth upon the two sides usually exhibit similar trends. There is no appreciable variation in the amount of dentine occurring within the

reentrant angles. In the smaller teeth of juveniles the angles may appear to be more acute and sharply defined than in adults, but this seems to be merely because of the difference in the size of the teeth and is not relative. There are, however, fluctuations in the exact form of the reentrant and salient angles, but these are haphazard and purely individual. If they have significance it is extremely obscure.

Any conclusions based upon the length of the teeth must be accepted with the greatest caution, for teeth are prone to become loose during cleaning of the skull and are then easily pushed in or pulled out beyond their normal positions. After drying, it is extremely difficult to detect such misplacement unless it be uneven. The length of the anterior molars in relation to the posterior ones, in both upper and lower series, is, of course, interdependent upon the length of the incisors and the configuration of both the upper and lower diastemata.

It is entirely permissible to presume that there is some slight fluctuation in the rate at which the teeth of different individuals grow from the persistent pulp, and there must also be variation in the rate at which the teeth are worn away, according to the habits of the individual and the character of the food consumed. Longer incisors, brought about by one of these causes, would therefore effect longer anterior cheek teeth, for these latter can not wear down more rapidly than the wear of the incisors permits.

INCISORS.—In the series at hand there is no relative variation in the incisors save in wear and size with age. As the skull increases in size so do the alveoli,

a b c

FIG. 23.—Individual variation in the pattern of the second upper molar $\frac{M2}{}$: *a*, No. 3825; *b*, No. 3815; *c*, No. 3804

and consequently the size of the persistent pulp cavities. Hence the incisors of adults are of a larger diameter and greater arc of curvature with the projection of the free portion correspondingly greater. With increased use of the incisors with age there is greater wear upon their posterior faces. The cutting points of the lower incisors in adults, however, are practically as sharp (acute) as in immatures; hence the pits upon the upper incisors are but a shade wider in the older animals, often leaving a thin splinter of enamel projecting upon the lateral edge of the upper incisors of the larger skulls.

Maxillary Molars

FIRST MOLAR.[5]—This tooth is composed of the usual anterior, crescentic loop, two inner, and two outer triangles, all closed. There is no appreciable variation in its pattern.

SECOND MOLAR.—This consists of an anterior crescentic loop, an inner and two outer triangles, all closed. Only the posterior space is variable. At one extreme is a tendency toward acute sharpness of the posterior enamel faces (fig. 23, *a*), but this condition is rare, occurring to a marked extent in but two or three examples. At the other extreme is a condition in which the posterior triangle has developed a slight though definite postero-internal loop (fig. 23, *c*) or spur (metaconule), the enamel space remaining open. This character is well developed in but two individuals, both females, but there is a trace of it present in 18

[5] The usual terminology of first, second, and third molars is employed.

others—7 males and 11 females. Needless to say, the allocation of a number of examples in regard to the presence or absence of such a trace is purely arbitrary. As this tendency is present to a greater or lesser extent in at least 30 per cent of the skulls, it is of considerable importance. The pattern which may be considered as normal is illustrated in figure 23, *b*.

THIRD MOLAR.—The normal pattern of this tooth consists of an anterior crescentic loop, two external, and one internal closed triangles, and posteriorly, two open, internal loops, highly variable in this species as in most other microtines. In 33 individuals the penultimate loop is rather constricted, and the posterior one is subtended by a distinct, intero-posterior notch (fig. 24, *e*). In two or three cases this indentation is sufficiently pronounced so that, in reality, one might consider that there are five internal salient angles instead of the usual four. As hardly any two individuals can be found in which this portion of the third molar is precisely duplicated, the allocation of many specimens is arbitrary; but this general type may be considered normal, as it is the one more often found than any other. It insensibly grades into another subtype of pattern, represented by 26 individuals, in which the posterior enamel space has no marked indentation (fig. 24, *d*). In a third type, represented by 5 specimens, the internal salient angle of the posterior enamel space is definitely hooked forward (fig. 24, *c*). In two skulls the posterior enamel space is exceedingly small, with-

FIG. 24.—Individual variation in the pattern of the third upper molar (M3: *a*, No. 3817; *b*, No. 3873; *c*, No. 3864; *d*, No. 3837; *e*, No. 3835

out indentations (fig. 24, *a*), and in one (fig. 24, *b*) the penultimate loop upon the right side, but not upon the left, is entirely closed, a condition that may be considered as aberrant. These five types of enamel pattern may be still further subdivided at the pleasure of the investigator, but nothing is to be gained thereby. There is also a tendency exhibited by a few individuals for other triangles to remain open, as illustrated by figure 24, *d*, and the posterior internal triangle is found in this condition not infrequently.

It is entirely impossible to correlate these variational trends with age or any other character, and they can be considered only as evidence that the third upper molar is at present much more unstable in an evolutional sense than either of the two other maxillary cheek teeth. This is the last of the upper teeth to emerge, and hence it is relatively less worn and developed in small juveniles than in older specimens.

Mandibular Molars

FIRST MOLAR.—As is the case with the majority of forms in this subfamily, the first lower molar is the most variable as well as the most complex of all the cheek teeth. It is in the anterior, tripartite enamel space that this diversity is encountered, and the variation is well nigh infinite. Truly no two are alike, nor is there bilateral symmetry between the two rami in this respect, for as often as not each ramus must be assigned to a different group. If it be attempted to establish too many groups for the different types of variants, however, a condition bordering on chaos results, with weakly-defined criteria for designation, and it is better to limit the number of main groups to three.

In the first group the outer lobe of the trisection is situated practically entirely posterior to the inner. All loops remain open, and each loop may vary widely in size and proportions. In this group, represented by figure 25, *a*, are 75 of the 132 rami.

In the second group, of which figure 25, *b* is typical, the outer lobe of the trisection is *not* practically entirely posterior to the inner, but in only a few cases is it situated just as far forward as the inner. All loops remain open in this group also, in which belong 48 of the rami.

Nine rami are assigned to the third group, illustrated by figure 25, *c* and *g*. In it the outer lobe of the trisection is situated posterior to the inner one and is entirely closed, forming a supplementary triangle upon that side of the tooth. In the remaining details of figure 25 are shown the more noteworthy variations of these three patterns.

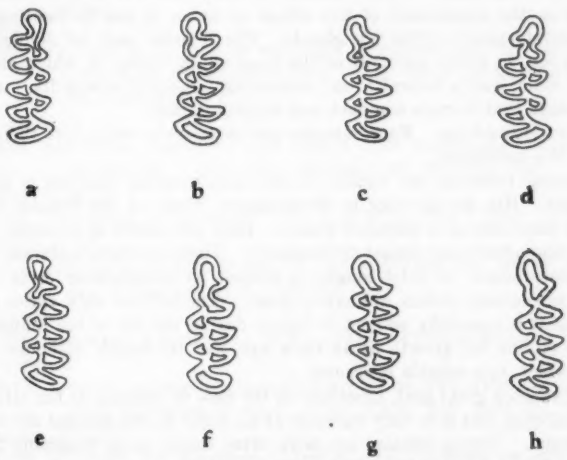


FIG. 25.—Individual variation in the pattern of the first lower molar. $\overline{M1}$: *a*, No. 3888; *d*, No. 3873; $\overline{M1}$: *b*, No. 3850; *c*, No. 3820; *e*, No. 3842; *f*, No. 3853; *g*, No. 3825; *h*, No. 3863

The writer is convinced that this great variation in tooth pattern within the series is without significance in the present connection, save, as in the case of the third upper molar, that it indicates evolutional instability at this point. As previously mentioned, additional subgroups might be designated in order to classify the variants with still finer exactness, but as the differences are purely individual and without connection with other characters, in so far as it is possible to see, they need not be dwelt upon in greater detail in the present paper.

The first lower molar, then, consists of a highly variable, tripartite division anteriorly, followed by two closed triangles upon the outer or buccal side and three upon the inner or lingual side, with a posterior crescentic loop. All these triangles are normally closed, exceptions occurring in two cases in which the anterior inner triangle remains open (fig. 25, *f*).

SECOND MOLAR.—This consists of two small outer triangles, two larger inner ones, and a posterior crescentic loop. There is no appreciable variation.

THIRD MOLAR.—In this tooth there are three simple, closed loops, the anterior one smallest and the other two progressively larger. The inner reentrant angles are deep, but the outer ones are barely indicated. There is no appreciable variation.

SUMMARY

This paper embodies the results of an intensive study of a large series of a meadow mouse, *Microtus montanus yosemite* Grinnell, undertaken to secure data on the amount of variation to be found in a single species of small mammal represented by specimens taken at the same place, within a short period, and by the same collector, thus insuring uniformity as regards preparation of material. It is believed that the results will furnish a criterion useful to later students of related groups of small rodents.

The series under discussion, consisting of 66 skins with skulls, besides spirit specimens, was collected at virtually one time and at a single spot, in Mono County, California. The conditions existing there were very uniform, and the locality unusually free from disturbing influences.

Coloration, especially of the females, is somewhat variable. Much of the difference in the appearance of the pelage of males is due to fighting and to varying development of the hip glands. The females may be divided into a grayish group, in which are most of the large adults, many of which are grayer than any male; and a brownish one, consisting largely of subadults. Juveniles have a pelage that is more compact and slightly darker.

The molt is insidious. Four females are excessively worn, but there are no males in this condition.

The plantar tubercles are variable in size and number, but five is the usual complement. Hip glands vary in development, those of old females being of about the same size as in subadult males. They are absent in juveniles and are probably dependent upon sexual development. There are eight mammae present.

The measurement of total length is subject to considerable error, and the variation in sexually mature animals is great. The tail not only varies much in length, but it is especially subject to injury during the life of the animal. The hind foot attains full growth at an early age, and its length, although varying to some extent, is a reliable character.

Weight varies a great deal, especially in the case of females, as the latter often contain embryos, but it is very valuable as an index to the general development of the animal. Young females are more often found to be pregnant than old ones, but with the latter the litters average larger.

Most of the individual variation of the skull is due to differences in the development of the muscles of mastication, and no thorough understanding of the osteology can be gained without some knowledge of the myology. Bones to which the main muscles are attached vary in response to stimulation by the latter. Other bones vary because of crowding.

The skull consists of the face and cranium proper, the latter being divisible into three rings, the anterior one of which is "dead center" of the skull. Skulls of juveniles are much weaker and more rounded than those of adults, and this, with lack of ridging in the former, accentuates the *appearance* of age difference to a greater extent than is actually found to be the case. The capacity of the braincase is, to all intents, proportionately the same at all ages.

The measurement of condylo-basilar length is the most satisfactory criterion for the arrangement of a series of skulls with respect to general development. Other composite measurements are of value as indices to the variation existing in divers portions of the skull and to indicate correlated trends. They vary in different degrees, both individually and with age. Variation in the precise configuration of the bones of the skull is, of course, infinite, such being the result of an enormous number of the most complicated developmental factors, only a very few of which can be partially defined.

Variation of the mandible is considerable, but the characters are usually correlated with other portions of the skull, and it is considered that most mandibular characters are relatively unimportant in systematic work when the skull proper is available.

The patterns of the first lower and third upper molars are excessively variable, but this is individual, and practically no part of it is due to age. It is felt that an undue phylogenetic importance has usually been ascribed to these differences within a group of species, but that in such aggregations of individuals as the present they point to nothing more than unstable evolutional trends.

LITERATURE CITED

(1) Adams, L. A.
1919. A memoir on the phylogeny of the jaw muscles in recent and fossil vertebrates. Ann. N. Y. Acad. Sci. 28: 51–166, illus.

(2) Allen. J. A.
1894. Cranial variation in Neotoma micropus due to growth and individual differentiation. Bul. Amer. Mus. Nat. Hist. 6: 233–246, illus.

(3) Bailey, V.
1924. Breeding, feeding, and other life habits of meadow mice (Microtus). Jour. Agr. Research 28: 523–535, illus.

(4) Cunningham, D. J.
1923. Textbook of anatomy. Ed. 5, 1577 p., illus. New York.

(5) Howell, A. B.
1923. Periodic fluctuations in the numbers of small mammals. Jour. Mammalogy 4: 149–155.

(6) Jayne, H.
1898. Mammalian anatomy. 815 p., illus. Philadelphia and London.

(7) Kellogg, R.
1922. A study of the californian forms of the Microtus montanus group of meadow mice. Univ. Calif. Pub. Zool. 21: 245–274.

(8) Parsons, F. G.
1896. Myology of rodents.—Part II. An account of the myology of myomorpha, together with a comparison of the muscles of the various suborders of rodents. Proc. Zool. Soc. London 1896: 159–192.

(9) Reighard, J. E., and Jennings, H. S.
1901. Anatomy of the cat. 498 p., illus. New York.

PLATE 1

Dorsal and ventral aspects, twice natural size, of adult No. 3856, immature No. 3880, and juvenile No. 3833, *of Microtus montanus yosemite* Grinnell, showing variation with age.

A
B
C
D
E
F

A GENETIC AND CYTOLOGICAL STUDY OF CERTAIN HYBRIDS OF WHEAT SPECIES[1]

By KARL SAX, *Biologist, Maine Agricultural Experiment Station*, and E. F. GAINES, *Cerealist, Washington Agricultural Experiment Station*

The cultivated species of wheat can be divided into three definite groups based on genetic, taxonomic, and cytological classification. Each of these groups has certain specific characteristics not found in the other groups. The Einkorn group is of no economic importance. The emmer group is of considerable economic importance in certain wheat-growing districts, while the vulgare group includes most of the varieties in common use. The emmer group in general possesses many desirable characteristics such as disease resistance, drought resistance, high protein content, and high yield under certain conditions. The vulgare group, on the other hand, is in general susceptible to disease and in most cases is not adapted to a semiarid climatic condition, but the only varieties of wheat which produce a high quality of grain are in this group. It is only natural that for many years plant breeders have attempted to combine the desirable characters of the emmer wheats with the high quality of the vulgare wheats. It would seem to be a simple problem to combine, for instance, the disease and drought resistance of the durum wheat with the high yield and bread-making qualities of certain vulgare wheats, but apparently no economic varieties have been obtained by combining the desirable characteristics of these two classes of wheat species. In the progeny of such crosses certain parental characters were found to be associated together, and it was difficult, or perhaps impossible, to obtain the desirable combinations in a single individual.

Crosses of wheat varieties which belong to different groups result in partially sterile F_1 plants and different degrees of sterility in F_2. Crosses between different species of the two groups result in different degrees of sterility. Some combinations show a very high degree of sterility while others are nearly as fertile as the parents.

A study of the chromosome behavior in such partially sterile hybrids has shown the reason for the sterility and why certain characters are more or less closely associated in the F_2 hybrids. The wheat species in the emmer group have 14 haploid chromosomes while those in the vulgare group have 21 haploid chromosomes. On crossing species of these two groups with different chromosome numbers an F_1 plant is obtained with 35 chromosomes in the somatic cells. In the reduction division of the F_1 there are 14 pairs of chromosomes and 7 single chromosomes. The 14 pairs of chromosomes undergo reduction in the usual manner, but the 7 single chromosomes are apparently distributed at random to one pole or the other, so that the gametes will contain from 14 to 21 chromosomes (*10*).[2] In most cases, at least, the perfection of the gametes increases as the chromosome number approaches 14 or 21, and the gametes with certain intermediate numbers are eliminated, due to sterility. Genetic investigations conducted in

[1] Received for publication Mar. 31, 1924—issued Nov., 1924.

[2] Reference is made by number (italic) to "Literature cited," pp. 1031–1032.

connection with cytological work indicates that the 7 additional chromosomes possessed by the vulgare group determine in some way the characteristic properties of that group. Thus it would be expected that segregates of such partially sterile hybrids would resemble the vulgare wheat if the segregates possess 21 chromosomes, while the 14 chromosome segregates would resemble the emmer group. The association of certain characters with chromosome number in F_1 would explain why certain characters are usually associated and why desirable characters of the two groups of species can not readily be combined.

Since there is considerable difference in the degree of sterility of certain species crosses it might be expected that the segregates from comparatively sterile crosses would tend to resemble more closely the parental form, while with increased fertility certain segregates might be obtained which would combine certain of the desirable properties of the two parental species. It may also be possible to determine the location of certain genetic factors in these hybrids. If, for instance, certain characters are determined by factors in the 14 primary chromosomes which pair in the species crosses, then these characters would be expected to segregate more or less normally. On the other hand, characters borne by the 7 additional chromosomes of the vulgare wheat would be expected to behave in a nonMendelian manner, due to the random distribution of a single set of chromosomes and more or less sterility of gametes and segregates with an intermediate chromosome number. Thus it should be possible to determine whether certain genetic factors are in the 14 primary chromosomes or are in the additional chromosomes of the vulgare species. A study has been made of the sterility, genetics, and cytology of a number of such species crosses with these objects in view.

MATERIAL AND METHODS

The parents used in this investigation include three species in the emmer group and two species in the vulgare group, as follows:

	Variety	Agronomic variety
EMMER GROUP		
Triticum polonicum L.	*villosum* Körn	Polish.
T. turgidum L.	*pseudo-cervinum* Körn.	Alaska.
T. Durum Desf.	*hordeiforme* Körn.	Kubanka.
VULGARE GROUP		
T. vulgare Vill.	*lutescens* Körn.	Marquis.
T. vulgare Vill.	*albidum* Körn.	Amby.
T. compactum Host.	*humboldtii* Körn.	Washington Hybrid 143.

In describing and referring to the varieties the agronomic name will be used. Spikes of the different varieties are shown in Plate 1. Following is a brief description of the varieties used. Alaska is a spring wheat, with branched spike, black awns 3 to 12 cm. long, kernels white and usually starchy. Polish is a spring wheat with black awns 4 to 10 cm. long, glumes and kernels very long, awns usually deciduous, kernels white, and very hard. Kubanka is a spring wheat with glumes and awns yellowish, awns from 6 to 15 cm. long, kernels white and very hard. These three varieties all belong to the emmer group and all have more or less pithy straw and sharply keeled glumes.

The varieties belonging to the vulgare group in all cases have hollow straw and the keel on the back of the glume is relatively small. Marquis is an early spring wheat and has yellowish glumes, hard, red grain, is considered awnless, but has a few apical awns 1 to 10 mm. long. Amby is an Australian wheat which is completely awnless and has white glumes and white kernels. Washington Hybrid 143 is a club wheat with very soft grain and apical awns 2 to 10 mm. long.

Crosses were made between Marquis × Kubanka, Hybrid 143 × Alaska, Marquis × Alaska, Hybrid 143 × Polish and Amby × Kubanka. The F_2 generation of each cross was grown at the Washington Agricultural Experiment Station, Pullman, Wash, in 1921. Conditions in eastern Washington are ideal for growing wheat for genetic studies, because the semiarid climate permits maturity without any discoloration of glumes or awns and the color characters can be studied readily. The percentage of segregates which will germinate and mature is also much higher than is the case in the Middle Western or Eastern States. Data on height, time of maturity, and per cent of sterility of the F_1 plants were obtained at the Washington Experiment Station. One head from each F_2 and F_3 plant was sent to the Maine Agricultural Station for a more detailed classification. A code was made for most characters, and all data were punched on cards so that the material could be analyzed with the aid of a sorting machine.[3]

In certain crosses each character was correlated with every other character to determine the degree of association between the different characters. The correlation ratio, the correlation coefficient, and the coefficient of contingency were used, depending on the nature of the data. In obtaining correlations between F_2 and F_3 the mean values of the F_3 families were used in most cases.

Certain of the intermediate types in F_3 were selected and grown for a cytological study in F_4.

STERILITY IN SPECIES CROSSES

The degree of sterility in each of the five crosses is shown for the different generations. In the F_1 of each cross the actual number of grains per spikelet was used, but in F_2 and F_3 only the grains in the two outer florets were considered, so that two grains per spikelet would be complete fertility. In the parent varieties the grains per spikelet ranged from about 1.7 to 2.

[3] The following code was used in describing F_3 and F_3 segregates:

A. Type of culm—
  1. Hollow.
  2. Intermediate.
  3. Solid.

B. Diameter of culm in millimeters.

C. Type of spike—
  1. Open.
  2. Intermediate.
  3. Compressed.

D. Type of glume—
  1. Slightly keeled.
  2. Medium keeled.
  3. Strongly keeled.

E. Shape of glume—
  1. Square.
  2. Medium.
  3. Pointed.

F. Color of glume—
  1. Yellow.
  2. Brown.
  3. Black.

G. Outer glume pubescence—
  1. Absent.
  2. Slight.
  3. Heavy.

H. Awned. Ranging from absent to those more than 10 cm. long. In F_3 the actual length of the longest awn was recorded.

I. Awn color—
  1. Yellow.
  2. Brown.
  3. Black.

J. Length of rachis in centimeters.

K. Texture of rachis—
  0. Strong.
  1. Intermediate.
  2. Brittle.

L. Number of spikelets.

M. Number of grains.

M. Number of grains per spikelet.

N. Grain length in millimeters.

O. Grain shape.

P. Grain color, ultimately classified as either white or red.

Q. Grain texture, starchy, intermediate, and very hard.

T. Type of head. Segregates were classed according to their resemblance to the different species of wheat, *vulgare*, *durum*, *spelta*, etc.

It is evident that there is considerable range in sterility of F_1 hybrids. In the cross Marquis × Alaska the F_1 plant was practically as fertile as either parent. The only indication of sterility was the wrinkled grain and the great range in size of the kernels. In F_2 the range in average sterility for the different crosses is less than the F_1, due partly to the greater number of individuals present. There seems to be little relation between sterility in F_1 and sterility in F_2. This result is not entirely unexpected since in the more sterile F_1 individuals only the more favorable combinations would survive, while in such crosses as Marquis × Alaska many of the gametic recombinations would survive and function more or less favorably. In the F_2, sterility is due not only to gametic incompatibility but also to differences in somatic development. Certain plants are so poorly developed that they set no grain, while others are extremely vigorous in vegetative development but are sterile, due to gametic imperfections. The difference in sterility in F_2 is significant. In the case of Marquis × Alaska the sterility is greater than in the cross Amby × Kubanka. This is partly due to climatic conditions, since the F_2 of Marquis × Alaska was grown in Washington State where a greater number of the weaker types undoubtedly survived, while the other cross was grown in Maine and only the strongest and most vigorous segregates could survive the extreme climatic conditions.

TABLE I.—*Sterility of various species crosses as indicated by average number of grains per spikelet (GS) in F_1, F_2, and F_3. The number (n) of individuals involved is indicated in each case*

Crosses	F_1		F_2		F_3	
	n	GS	n	GS	n	GS
Marquis × Kubanka	13	1.05±0.08	135	0.80±0.03		
Hybrid 143 × Alaska	34	1.09± .05	293	.63± .02		
Marquis × Alaska	8	2.00± .16	152	.98± .03	1536	1.09±0.01
Hybrid 143 × Polish	19	.66± .06	82	.70± .04		
Amby × Kubanka	8	.58± .03	52	1.07± .06	38	1.59± .04

It has been found that gametic and somatic sterility is closely associated with chromosome behavior. Those individuals with their chromosome number approaching either 14 or 21 survived more frequently than the individuals with an intermediate chromosome number. Thus it would be expected that where there was a high degree of sterility in F_1 the segregates with an intermediate chromosome number would be more rapidly eliminated, while in the relatively fertile combinations segregates with an intermediate number might survive in many cases and a relatively high degree of sterility would persist for a number of generations, although complete sterility would be comparatively rare. This hypothesis can probably be checked by an analysis of genetic behavior. For instance, in the more sterile combinations one might expect to find a higher correlation between the various characters due to the elimination of intermediate types. In such a case the surviving segregates would resemble the emmer parent or the vulgare parent and the characteristic features of the two groups would be more or less closely associated. In less sterile individuals the intermediate type would be expected to survive to a considerable extent, so that the vulgare and emmer characteristics might be combined in many cases and there would then be little correlation between the characteristic features of the two groups. One might also expect the recovery of occasional segregates combining the desirable characters of the two species in the more fertile combinations, while in more sterile hybrids the only homozygous fertile segregates would resemble one parent or the other. The available data do not, however, indicate

that segregates with a chromosome number intermediate between 14 and 21 can be obtained in a completely fertile and homozygous condition.

GENETIC INHERITANCE IN SPECIES CROSSES

Most of the characters studied in these various crosses do not appear to segregate in a simple Mendelian manner, and the percentage of homozygous individuals resembling one parent or the other are in most cases comparatively small. In the case of the cross Marquis × Alaska, the F_2 classification has been checked by growing the F_3 and the same general conclusions have been verified. There are, however, two or three characters which seem to segregate in the usual Mendelian manner, indicating perhaps that these characters are dependent on factors in the 14 primary chromosomes which behave in a normal manner in the reduction division. Some of the more typical characters are shown in Table II, to illustrate the inheritance of those characters which seem to segregate in a Mendelian manner and those which show no clear segregation into definite Mendelian ratios.

TABLE II.—*Segregation of certain characters in F_2 of various crosses of wheat species*

Cross	Length of awns in centimeters					
	Tips					
	1	2-3	4-10	4-10	10+	n
1. Marquis × Kubanka	48	53	9	17	8	135
2. Hybrid 143 × Alaska	188	36	8	57	3	292
3. Marquis × Alaska	65	42	14	14	17	152
4. Hybrid 143 × Polish	48	11	5	13	5	82
5. Amby × Kubanka	36	10	----------	2	4	52

TYPE OF KEEL

Cross	Vulgare	Intermediate	Durum	n
1	36	55	44	135
2	86	87	120	293
3	38	85	29	152
4	7	56	19	82
5	15	26	11	52

AWN COLOR

Cross	Yellow	Brown	Black	n
2	105	56	84	245
3	77	13	62	152

GRAIN TEXTURE

Cross	Very hard	Hard	Intermediate	Starchy	Very starchy	n
1	50	63	3	1	----------	117
2	24	51	----------	77	47	199
3	24	76	36	9	2	147
4	21	41	2	----------	4	68
5	1	26	6	9	7	49

In the description of the various F_2 segregates the length of the awn was arbitrarily grouped into five classes as indicated in Table II. Individuals with awns from 1 to 3 cm. long when awned only at the tip would ordinarily be classed as awnless segregates. Those with awns from 4 to 10 cm. in length when found at the tips only might be considered in some cases as intermediate, although the awnless condition is more or less dominant in wheat crosses. Segregates with awns from 4 to 10 cm. in length resembled the awned vulgare wheat, while individuals with awns greater than 10 cm. in length could be classed as the emmer type of awn. In the first four crosses there is a rough approximation to a 3:1 ratio of awnless to awned. In the fifth cross, Amby × Kubanka, the percentage of awned individuals is relatively low. Amby is a completely awnless wheat and the Howards (*8*) have found that a true awnless wheat crossed with an individual with long awns results in a 15:1 ratio. In this cross of Amby × Kubanka the ratio more closely approximates the 15:1 ratio than it does the 3:1 ratio.

In general, segregates of crosses between emmer and vulgare wheats can be classified as the emmer type or vulgare type according to the shape of the keel. In the F_2 segregation of keel type is apparently dependent on a single Mendelian factor in some cases, but the classification is more or less arbitrary and the F_1 behavior does not indicate a single factor difference for this pair of characters.

In the crosses involving Alaska it was possible to classify the segregates according to color of awn. Even in the so-called awnless segregates the length of the awn was sufficient to indicate the color present. The classification of awn color is very difficult because climatic conditions in many cases apparently inhibit the development of the black color, and even in parental varieties the color may appear in some individuals and be absent in others. The classification of certain individuals as brown is not definite but simply indicates that they could hardly be classed as yellow or black. Although the F_2 segregation does not indicate any simple Mendelian segregation, the F_3 generation of Marquis × Alaska does indicate a single factor difference.

Grain texture is one of the characters which is unusually difficult to classify. The texture of the grain was determined in most cases from a single head of each plant in F_2 and F_3. Subsequent work during the past winter has shown that on a single plant certain heads may bear grain, all of which would rank as hard, while other heads of the same plant would have only soft grain. This character is apparently dependent on environmental conditions to such an extent that no satisfactory genetic analysis can be made of this character, at least in these species hybrids. In most of the crosses described the emmer parent had extremely hard grain, while the vulgare parent has relatively soft grain. The condition is apparently reversed in the case of Marquis × Alaska, however, because the Marquis has comparatively hard grain, while Alaska has a starchy grain due apparently to the factor for yellowberry. When the factor for yellowberry in Alaska is eliminated Alaska has grain practically as hard as the other species in the emmer group. This is indicated by the fact that flinty grains are found in certain segregates in F_2 and F_3.

The cross Marquis × Alaska was carried to the F_3, and 1,536 F_3 individuals were analyzed. A study of the various F_3 families indicates the true genetic nature of the F_2 segregates and permits an accurate classification of the F_2 generation. For most characters 110 F_2 segregates are represented in F_3, although for certain grain characters fewer individuals are available, due to partial or complete sterility in F_3. The F_2 behavior, as indicated by F_3 segregation, is shown in Table III.

TABLE III.—*Marquis × Alaska—F_2 behavior as indicated by F_3 segregation; showing the number of F_2 families which breed true for the alternative characters, and the number which show segregation*

Characters studied	Behavior of F_2 families			n
Awning	Awnless.	Segregating.	Awned.	
Actual number	28	51	31	110
Theoretical for 3:1 ratio	27.5	55	27.5	
Awn color	Yellow.	Segregating.	Black.	
Actual number	26	66	18	110
Theoretical for 3:1 ratio	27.5	55	27.5	
Grain texture	Hard.	Segregating.	Soft.	
Actual number	10	80	8	98
Spike shape	Normal.	Segregating.	Branched.	
Actual number	17	89	4	110
Type keel	Vulgare.	Segregating.	Durum.	
Actual number	13	96	1	110
Grain color	Red.	Segregating.	White.	
Actual number	32	56	6	94

If no segregation occurred in seven or eight or more F_3 individuals of a certain family the F_2 parent was considered homozygous for the character involved (assuming a single factor to be involved). In this way the different F_2 individuals could be classed as homozygous for one character or the other or heterozygous as indicated by F_3 segregation.

When all F_3 plants of a given family had an awn length of less than 3 cm. the F^2 was considered homozygous for the awnless condition. It was found that all of the F_2 individuals in the first two classes bred true for awnless or segregated into awned or awnless in the F_3. Some of the individuals are classed as having awns from 4 to 10 cm. long on the tips in the F_2 bred true for awns in F_3, while a few of them segregated into awned and awnless. All of the F_2 individuals which had awns 4 cm. and longer distributed the entire length of the spike bred true for the awned condition in F_3. The segregation of the awned condition as shown in Table III clearly indicates a simple one-factor difference for so-called awnless and awned segregates in F_2. This behavior is in accord with results found in varietal crosses (*4*, *7*, *8*, *9*).

Although it is practically impossible to accurately classify awn color in F_2 due to the effect of environmental factors, it is comparatively easy to classify the F_2 segregates based on F_3 behavior. The effect of environmental factors is undoubtedly responsible for the excess of individuals classified as segregating. No doubt a certain number of these individuals are genetically black, but climatic conditions in some way inhibit the black color from appearing in certain individuals, so the F_3 family was classed as segregating into black and yellow. There is, however, little question but that here again a simple factor for black versus yellow or brown is involved.

A great majority of F_3 families showed segregation for grain texture. Only 10 individuals were homozygous for hard grain and 8 homozygous for soft grain. There is, apparently, no simple Mendelian factor difference involved in this case.

Individuals were also classified according to shape of spike, whether normal or branched. In the F_2 there were several individuals which were quite similar to the Alaska, at least in the morphological appearance of the spike. In F_3 five segregates out of 152 were classed as branched while 48 were classed as partially branched, that is, showed some tendency of branching of a few spikelets. It is evident, then, that the normal condition is partially dominant over the branched condition. All of the completely branched individuals in F_3 which resembled the Alaska parent to some extent, bred true in F_3. There is in this case no indication of simple Mendelian segregation.

Only one F_3 family bred true for the emmer type of keel, while 13 families were homozygous for the vulgare type of keel. Most of the individuals were apparently heterozygous and there is no indication of a simple ratio.

Grain color is a very difficult character to classify in F_2, due to different degrees of hardness of the grain. A very hard endosperm will give the grain an amber appearance, which may sometimes be mistaken for red. However, the F_3 behavior indicates the true genetic composition of the F_2 individuals and the classification of F_3 families into homozygous and heterozygous types is less difficult. All individuals classed as light amber in the original code have been considered as white in the present classification. The segregation approximates very closely that expected for a two-factor difference, the number of homozygous whites being practically 1 in 16 F_2 segregates. If two factors for red grain are involved in this cross, however, there should be a much larger proportion of the F_3 families breeding true for red. There should be forty-two F_3 families breeding true for red and forty-eight families segregating either into 15 : 1 or 3: 1. Also due to the paucity of the individuals in F_2 families, the twenty-four families which should show a 15 : 1 segregation would in many cases be classed as homozygous for at least one factor for red, so that the proportion of red should be in excess of 42, which does not agree with the actual data.

The F_2 segregates were also classified in respect to type of head, whether they resembled *vulgare*, *compactum*, *Spelta*, etc. The types which bred true in the third generation included 4 *vulgare*, 1 *Spelta*, 2 *durum*, 2 *dicoccum*, and 1 classed as abnormal. There were also two *compactum* segregates in F_2 which bred true to the type in F_3, but it is probable that these plants were mixtures, as they were completely fertile in all cases in both F_2 and F_3 and were extremely uniform in all characters.

The date of ripening in F_3 ranged from the 10th of August to the 9th of September. Only eighteen F_3 families were apparently homozygous for date of ripening. Fourteen families which were homozygous ripened between the 10th and 13th of August while most of the heterozygous segregates had a mean date of ripening ranging from August 13 to September 9. There was some correlation in F_3 between type of spike and date ripe. The *Spelta* segregates ripened earlier than the abnormal types which could not be classified.

A number of correlations between various factors were obtained in F_3, and between the F_2 individuals and F_3 families of the cross Marquis × Alaska. Segregates in F_2 which were comparatively sterile were also relatively sterile in F_3 while the more fertile F_2 individuals resulted in comparatively fertile progeny in F_3. The correlation between grains per spikelet in F_2 and grains per spikelet in F_3 was $.54 \pm .05$. There was also considerable correlation between the various characters of F_2 and F_3 segregates. For instance, culm type in F_2 correlated with culm diameter in F_3 gave a correlation ratio of $.59 \pm .04$. Type of keel in F_2 correlated with keel type in F_3, using the coefficient of contingency, gave a value of $.52 + .06$. Height of plants in F_3 correlated with date ripe in F_3 gave a value of $r = -.18 \pm .06$, indicating that vegetative vigor had little relation to the date of maturity. There was some tendency for the more fertile F_3 segregates to ripen earlier, as indicated by the value of $r = -.25 \pm .06$. In these various cases the mean value of the F_3 families was taken. Using all of the 1536 F_3 segregates a correlation of $.62 \pm .01$ was found between grains per spikelet and height, indicating that fertility increased as the vegetative vigor increased and that much of the sterility was associated with poor vegetative development.

It might be expected that F_3 segregates resembling the parent would be somewhat more fertile than intermediate or abnormal types. In Table IV the various types of segregates are shown, the number of such segregates, and the average

number of grains per spikelet. Segregates resembling the Alaska parent are the most fertile, followed by those resembling the vulgare parent. The intermediate types which could be placed in no particular group were the most nearly sterile.

TABLE IV.—*Segregation and average fertility of various types of F_2 segregates in Marquis × Alaska*

Type head	Number	Grains per spikelet
1. Vulgare	426	1.43
3. Spelta	155	1.18
4. Durum	307	1.23
5. Turgidum	49	1.70
6. Emmer	154	1.33
9. Abnormal	429	.81

The various types of segregates obtained in the F_2 of Marquis × Alaska and in the cross Hybrid 143 × Polish are shown in Plate 1. In the first case segregates are obtained which resemble either parent and also individuals which resemble *T. spelta* and *T. durum*. Types resembling *T. compactum* were also obtained but these may be due to mixtures. In the second cross types similar to *T. durum* were obtained as well as a number of types unlike any cultivated species. The segregates with very long glumes but with short heads as shown in Plate 1, C, *b* were found to be quite sterile in most cases.

THE ASSOCIATION OF VARIOUS CHARACTERS IN SPECIES HYBRIDS

It has been pointed out that in the more sterile hybrids the intermediate types would be more rapidly eliminated and the surviving segregates in F_2 and F_3 might resemble the parental types more or less closely. In more fertile crosses, on the other hand, the intermediate types might survive for several generations and gradually become eliminated only after a number of years. Since certain characters are found only in the emmer wheats and other characters are found only in the vulgare wheats one might expect a higher degree of association of these characters in F_2 segregates of relatively sterile hybrids, while there would be comparatively little association of parental characters in the more fertile F_2 segregates due to the fact that the intermediate types are not so rapidly eliminated. Thus, for instance, in one cross the F_2 and F_3 segregates consist largely of individuals with approximately 14 or 21 chromosomes, and there would be little opportunity for combinations to occur possessing characteristics of both parental groups. If, on the other hand, the cross resulted in an F_2 progeny which was relatively fertile and included many types with an intermediate chromosome number, then there would be more or less combination of parental characters and less association between the characters peculiar to each group.

TABLE V.—*Correlation between various characters of 52 F_2 segregates of Amby × Kubanka and of 152 F_2 segregates of Marquis × Alaska*

Characters correlated	Amby × Kubanka	Marquis × Alaska
	Correlations	*Correlations*
Type of culm and—		
Type of keel	0.86±0.03	0.24±0.05
Shape of spikelet	.90± .03	.23± .06
Awn length	.80± .04	.27± .06
Grain texture	.68± .07	.48± .05
Type of keel and—		
Shape of spikelet	.84± .03	.39± .05
Awn length	.74± .04	.30± .05
Compactness of head	.24± .09	.26± .05
Grain texture	.80± .03	.17± .05
Grain shape	.90± .02	.12± .06
Shape of spikelet and—		
Grain shape	.89± .02	.07± .06
Grain texture	.69± .05	.28± .06
Length of awns and—		
Grain shape	.36± .08	.23± .05
Grain texture	.49± .07	−.13± .05
Grains per spikelet and—		
Type of culm	.40± .08	.11± .05
Type of keel	.53± .07	.32± .05
Homozygous factors	.42± .08	.03± .05
Do	−.02± .09	.03± .05
Heterozygous factors	−.19± .09	−.08± .05

Correlations between various characters of a comparatively sterile cross, Amby × Kubanka, and a comparatively fertile cross, Marquis × Alaska, are shown in Table V. The various characters, type of culm, type of keel, shape of spikelet, and in most cases awn length and grain texture, are all characters which differ greatly in the emmer and vulgare groups and these characters in each group are more or less characteristic and are not found in varieties within the other group. In the cross Amby × Kubanka the correlation between the various characters is rather high in all cases, indicating considerable association of the parental characters. In the more fertile cross, Marquis × Alaska, the correlations are in most cases relatively low or are of little or no significance. In the correlation between type of culm and grain texture the correlation is relatively high. Although Marquis has a harder grain than Alaska when grown in eastern Washington, the durum and emmer segregates usually had flinty kernels harder than those of Marquis. This is due to the fact that Alaska has hard grain if the factors for "yellowberry" are absent. These correlations show clearly that in the more sterile hybrids the parental characters are more or less closely associated, while there is less association as fertility increases. It is possible, of course, that ultimately the more fertile hybrid would result in segregates resembling one parent or the other, and that the elimination of intermediate types occurs more slowly in the more fertile combinations. This is indicated by the degrees of sterility found in various types of segregates, as shown in Table IV. The abnormal types which do not resemble any of the economic species are the most sterile while segregates resembling the parent species are the most fertile.

One might expect the segregates resembling the parent to be more fertile than the intermediate types. This is found to be the case in the cross Amby × Kubanka, as indicated by the correlation between grains per spikelet and type of culm. The culm type and keel type resembling these parental forms are associated with comparatively fertile individuals, while the intermediate forms are associated with relatively sterile individuals in F_2. In the cross Marquis × Alaska there was, however, little correlation between fertility and type of segregate. An attempt was also made to classify the various individuals according to the number of homozygous and heterozygous factors for the various characters involved. There is some indication in the first cross that with the increase in the number of homozygous factors the number of grains per spikelet is increased,

but the correlations are neither high nor consistent. In the second cross there are no significant correlations between fertility and number of homozygous or heterozygous factors. This method is not entirely satisfactory, however, since many factors might be in a heterozygous condition without resulting in any qualitative differences which can be described and tabulated.

It would appear from these results that segregates combining the desirable characters of the emmer group and the vulgare group can rarely be obtained in the comparatively sterile combinations, but that in the more fertile crosses such individuals might be obtained more frequently. It has previously been found that there is a very high degree of association between the various characters of the emmer and vulgare wheat in hybrid segregates (*11*). It is found, for instance, that most of the segregates which are rust resistant also resemble the durum or emmer parent in morphological characters and quality of grain. However, several vulgare segregates which were rust resistant were found in about 20,000 F_2 and F_3 segregates of crosses between wheats in the emmer and vulgare groups (*7*). None of these segregates was of economic value, however. By using species which result in relatively fertile segregates the probabilities of obtaining F_2 segregates which would combine the desirable characters of the emmer and vulgare wheats would be greatly increased, although it is not known at the present time how fertile and homozygous these types might be in subsequent generations. It is possible that ultimately all of the intermediate types would be eliminated, although Sevier wheat is an economic variety combining several durum and vulgare characters.

In comparing the genetic behavior of certain characters in the species hybrids it is also desirable to know how these same characters behave in fertile varietal crosses. Such characters as awn length, color of awns, color of grain and pubescence, and in certain cases hardness of grain, have been found to be dependent on Mendelian factor differences in varietal crosses within the vulgare group. It is obvious that certain characters used in species crosses can not readily be analyzed in fertile crosses because the characters are more or less common to the entire group. Such characters, for instance, as size of keel, extremely flinty grain, pithy culms and very long awns are found only in the emmer group and in very few cases are any of these characters absent in any variety within the emmer series. It is true that a few beardless varieties of durum and emmer wheats exist, but these have been derived for the most part, if not entirely, from crosses between members of the emmer group with members of the vulgare group. There is, however, one character which is found in Alaska and in none of the other varieties of the emmer group. This is the branching habit of the spike. An analysis of the behavior of this character was obtained from data on a cross between Alaska × Spring emmer. The F_1 was slightly branched although the F_1 plants frequently had some heads which were normal. In F_2 the segregates showed 294 normal to 107 branched. Only six of the F_2 plants were branching to the same extent as the Alaska parent. The degree of branching varied all the way from a reduplication of one or two spikelets to individuals which closely resembled the branched parent. The fact that there is much greater variation in the branched segregates, which are apparently recessive, is not unusual, as in *Chelidonium* doubleness is a recessive character and yet the doubles vary enormously while the singles do not vary at all in regard to petal number. The genetic behavior of this cross is being continued into F_3 for verification of F_2 classification. At any rate, it is evident that the genetic behavior in the varietal cross is entirely different than it is in the species cross. In the cross between Marquis × Alaska only five individuals were classed as branched in a population of 152 plants. In F_3 17 families bred true for normal, 89 segregated, and only 4 bred true for the branched condition.

THE RELATION OF CHROMOSOME NUMBER TO MORPHOLOGICAL CHARACTERS IN F_3 AND F_4 SEGREGATES

It has been found that the segregates of emmer X vulgare wheat which resemble the emmer parent have 14 chromosomes, while those which resemble the vulgare parent have 21 chromosomes and that the segregates with an intermediate number of chromosomes tend to become eliminated, due to sterility (*11*).

In a previous study a number of F_3 segregates were found which had an intermediate chromosome number and others were found which had intermediate head type. In some cases the segregates which were recorded as having intermediate chromosome numbers were of the durum or vulgare type. In one case a segregate was classed as a durum type but had 21 chromosomes. It was considered desirable to determine if the intermediate chromosome numbers and intermediate plant types persisted in the fourth generation, and to obtain additional data in regard to the relation between chromosome number and type of spike. One might also expect a larger proportion of F_3 and F_4 segregates to have a chromosome number of 14 or 21 in Amby × Kubanka than would be the case in the more fertile cross of Marquis × Alaska, where it might be expected that a comparatively large proportion of the segregates would be intermediate in chromosomes number as well as morphological characters. The F_4 segregates of these intermediate types for both Amby × Kubanka and Marquis × Alaska were grown in Maine in 1923. Chromosome counts were obtained with the use of Belling's method (*1*). It was not always possible to distinguish the univalent chromosomes from the bivalent, so that the numbers of chromosomes of each type could not be exactly determined. The descriptions of the F_3 and F_4 segregated of each cross, the chromosome number where it has been determined and the fertility of the F_4 segregates are shown in Table VI.

TABLE VI.—*Type of F_2 and F_3 segregates and chromosome number, grains per spikelet (g) shown for F_4 plants. The numbers and letters correspond to numbers and letters of types of F_2 plants shown in Plates 1 and 2. S=single chromosomes*

AMBY × KUBANKA

No.	Description, 1922, F_3	Chromosome No.	Description, 1923, F_4	Chromosome No.	g
	Plate 2				
1	Durum type	±16	Durum type	14	1.9
2	do		do	14	1.8
3	do		do	14	1.9
4	do		do	14	0
5	do	±16	do	14	1.9
6	do	14+4−6 S	do	14	1.1
7	Intermediate	14+3−4 S	Intermediate	18+2−4 S	1.3
8	Vulgare type	18	Vulgare type head—durum awns and grain	21	2.0
9	Intermediate	21	Vulgare type	20+1−2 S	1.5
10	do	21	do	21	2.0

MARQUIS × ALASKA

	F_3	F_4		
	Plate 1			
a	Durum head-vulgare keel	Durum head—vulgare keel	14	0.8
b	Durum head-soft grain	Durum head—soft grain	14	2.0
c	do	do	14	1.6
d	Vulgare head—durum keel	Branching head—hard grain	18+2−3 S	1.5
e	Vulgare head—durum keel and awns.	Vulgare head—durum keel and awns	18+2−3 S	1.5
f	do	Branching head—intermediate keel	18+2 S	.5
g	Vulgare head—intermediate keel—durum awns.	Vulgare head—durum awns, soft grain, intermediate keel.	19+2−3 S	2.0
h	do	Vulgare head—intermediate keel—hard grain	19+2−3 S	2.0

In the cross Amby × Kubanka several F_3 segregates were classed as the durum or intermediate type but had more than 14 chromosomes. Number 6, for instance, was classed as a durum type in F_3 and had 14 bivalent and 5 or 6 single chromosomes (S), a total of about 20 haploid chromosomes. When these various segregates were carried to F_4 it was found that all of them had 14 chromosomes and were all of the durum type. The fertility varied greatly, ranging from 0 grains per spikelet to individuals as fertile as the parent. Number 7, which was classed as intermediate in F_3 and also had an intermediate number of chromosomes, was intermediate and had an intermediate chromosome number in F_4. This individual was relatively sterile in F_4. One vulgare type recorded as having 18 chromosomes in F_3 was found to have 21 chromosomes in F_4, but had the typical durum awns and the hard grain typical of Kubanka. It was also as fertile as the parent. This case is unusually interesting because apparently two characters peculiar to the durum group are found in a 21 chromosome segregate. Whether or not this individual will be found homozygous and completely fertile in later generations is, of course, questionable. Two F_3 segregates classed as intermediate and with 21 chromosomes were found to segregate vulgare types of spikes in F_4 and had approximately 21 chromosomes each. Pictures of these F_4 segregates are shown in Plate 2 and are arranged in the same order as they are in the Table.

In the cross Marquis × Alaska a number of F_3 segregates were selected which appeared to be intermediate and which possessed combinations of durum and vulgare characters. In F_4 certain of these segregates maintained the combination of parental characters and in most cases had an intermediate number of chromosomes, usually with several single lagging chromosomes at the time of the reduction division. One segregate in F_4 had a durum type of head but with the small vulgare type of keel (Plate 1). This individual had 14 chromosomes, but was relatively sterile, as indicated by the number of grains per spikelet. An unusual combination was found with a durum head type but with soft grain. This individual had 14 chromosomes and was practically as fertile as the parent. The other F_4 segregates for which chromosome counts were made were found to have an intermediate chromosome number and ranged in fertility from 0.5 grains per spikelet to 2 grains per spikelet. Number 7, in F_4, had wrinkled grain, indicating its heterozygous condition and undoubtedly its progeny in F_5 would show various degrees of sterility. It will be of interest to follow these intermediate types into future generations and determine the relation of morphological characters and chromosome numbers.

There are several cases where the characteristics of the two parents are combined in a single individual and this individual may possess the parental chromosome numbers of 14 or 21. These results may indicate that in rare cases segregates can be recovered combining certain of the parental characters. Practical breeding experiments made in an attempt to combine the desirable characters of the emmer wheats with the bread-making qualities and yield of the vulgare wheats indicate, however, that the possibilities of recovering such intermediate types are rare and that the best results can be obtained by selecting the parental varieties within the vulgare group (*2, 9, 12, 4, 5, 6*).

CONCLUSIONS

Crosses between wheat species of the emmer group with 14 chromosomes, with members of the vulgare group with 21 chromosomes, result in partially sterile F_1 hybrids, and all degrees of sterility in F_2. Previous cytological studies of chromosome number and behavior in F_1 and F_2 indicate that gametes and segregates with an intermediate chromosome number tend to be eliminated

through sterility and that the ultimate homozygous fertile segregates will have either 14 or 21 chromosomes (*10*, *11*). Segregates with 14 chromosomes resemble the emmer parent in most respects while segregates with 21 chromosomes possess most of the vulgare characters, indicating that the 7 additional chromosomes determine the differentiating characters of the vulgare wheats.

The elimination of gametes and segregates with an intermediate chromosome number would disturb genetic segregation in case of factors located in the 7 chromosomes contributed by the vulgare parent which do not pair in the reduction division of F_1 crosses between emmer and vulgare wheats. Normal Mendelian segregation should usually occur with those factors located in the 14 emmer and vulgare chromosomes which pair in F_1 hybrids. Thus one might expect normal Mendelian segregation of characters common to the two groups of wheat species and aberrant segregation of characters which distinguish the two groups. Of the characters analyzed in both F_2 and F_3 of such species crosses, the presence or absence of awns, yellow or black awns, and red and white grain are all characters found in either the emmer group or the vulgare group although black awns are rare in vulgare wheats (*3*, *9*). The segregation of awn length into so-called awnless (tip-awned) and awned is clearly dependent on a single factor difference and a normal Mendelian segregation is obtained. The segregation of awn color is complicated by the effect of environmental factors but F_2 classification indicates a simple Mendelian ratio. The number of segregates with white grain in the cross of Marquis × Alaska would indicate the presence of two factors for red color although the number of segregating individuals is greater than expected.

On the other hand, the characters which distinguish the emmer and vulgare groups apparently do not segregate in a Mendelian fashion, as indicated by the data presented in Tables II and III. Most varieties of the emmer group have very hard flinty kernels, a large sharp keel on the outer glume and some varieties have branched spikes. These characters are found in no vulgare variety. Since these characters are common to all of the varieties in the emmer group it is impossible to determine how they are inherited in fertile varietal crosses. There is, however, one exception in the case of Alaska. Alaska has the branched spike while the durums and emmer wheats have a normal spike. The fact that the cross of Alaska × Emmer resulted in an apparently simple ratio of normal and branched or at least the genetic behavior is entirely different than in the species hybrids. The nonMendelian segregation of these typical emmer characters in the species hybrids suggests that they may be dependent on the presence or absence of factors located in the extra seven vulgare chromosomes which do not pair in crosses with emmer wheat. Since these seven chromosomes are irregularly distributed and certain classes are apparently eliminated due to sterility, a normal Mendelian segregation would not be expected.

Certain crosses between members of the vulgare group and members of the emmer group are more fertile than others as indicated in Table I. In the more fertile crosses segregates may possess certain combinations of parental characters and intermediate chromosome numbers while in the more sterile crosses the intermediate types would be rapidly eliminated and the surviving segregates would have either 14 or 21 chromosomes and would resemble the parental species. Thus there should be considerable correlation or association of the characters contributed by each parent in the more sterile hybrids while in the more fertile crosses there would be less tendency for the characters of each parent to be associated. This is actually the case, as indicated by the correlations presented in Table V. These results would indicate that combinations of the characters of the emmer and vulgare wheats can be obtained more frequently in the more fertile combinations. However, many plant breeders have attempted to com-

bine the drought and disease resistance of the emmer species with the high quality of the vulgare wheats without successful results.

In general, the intermediate types of segregates are more sterile than segregates resembling one parent or the other (Tables IV and V). Individuals resembling one economic species of wheat are more fertile than those which can not be so classed.

There is a greater proportion of intermediate types in the more fertile species hybrids, which may indicate that more of the segregates can function with an intermediate chromosome number in such crosses. A cytological examination of F_4 segregates shows that the intermediate types usually have an intermediate chromosome number but some of the segregates with 14 and 21 chromosomes also possess characteristics of both parents. The presence of some of the typical vulgare characters in 14 chromosome segregates and the occasional recovery of emmer characters in 21 chromosome segregates suggest that the chromosomes which carry the factors for the distinguishing vulgare characters may in some cases at least pair with certain of the emmer chromosomes in crosses between members of the two groups. The combinations of typical emmer and vulgare characters in certain segregates indicates that the differentiating vulgare characters are determined by factors in individual chromosomes and not by the combined effect of the additional seven chromosomes.

Although in the more fertile crosses there are many segregates with intermediate chromosome numbers it is questionable if such segregates can persist in a homozygous fertile condition. Certain combinations of emmer and vulgare characters do occur in segregates with 14 or 21 chromosomes and it is probable that a small proportion of segregates can be obtained which will combine certain characters of the two groups of species, especially in the more fertile combinations. From a practical standpoint, however, it would probably be more feasible to combine disease resistance and yield and quality of grain by selecting the parents within the vulgare group. It is perhaps significant that crosses or vulgare varieties are apparently the only ones which have resulted in new varieties of economic importance.

LITERATURE CITED

(1) Belling, J.
1921. On counting chromosomes in pollen-mother cells. Amer. Nat. 55: 573–574.

(2) Biffen, R. H.
1912. Studies in the inheritance of disease resistance. II. Jour. Agr. Sci. 4: 421–429.

(3) Clark, J. A., Martin, J. H., and Ball, C. R.
1922. Classification of American wheats. U. S. Dept. Agr. Bul. 1074, 238 p., illus.

(4) Gaines, E. F.
1917. Inheritance in wheat, barley, and oat hybrids. Wash. Agr. Exp. Sta. Bul. 135, 61 p., illus.

(5) ———
1920. The inheritance of resistance to bunt or stinking smut of wheat. Jour. Amer. Soc. Agron. 12: 124–132.

(6) Hayes, H. K., Parker, J. H., and Kurtzweil, C.
1920. Genetics of rust resistance in crosses of varieties of Triticum vulgare with varieties of T. durum and T. dicoccum. Jour. Agr. Research 19: 523–542.

(7) HAYES, H. K., and GARBER, R. J.
1921. BREEDING CROP PLANTS. 328 p., illus. New York.

(8) HOWARD, A., and HOWARD, G. L. C.
1915. ON THE INHERITANCE OF SOME CHARACTERS IN WHEAT. II. Mem. Dept. Agr. India Bot. Ser. 7: 273–285, illus.

(9) PERCIVAL, J.
1921. THE WHEAT PLANT. 463 p., illus. London.

(10) SAX, K.
1921. STERILITY IN WHEAT HYBRIDS. II. CHROMOSOME BEHAVIOR IN PARTIALLY STERILE HYBRIDS. Genetics 7: 513–552, illus.

(11) ———
1923. THE RELATION BETWEEN CHROMOSOME NUMBER, MORPHOLOGICAL CHARACTERS AND RUST RESISTANCE IN SEGREGATES OF PARTIALLY STERILE WHEAT HYBRIDS. Genetics 8: 301–321, illus.

(12) SPILLMAN, W. J.
1909. THE HYBRID WHEATS. Wash. Agr. Exp. Sta. Bul. 89, 27 p., illus.

PLATE 1

Parental varieties used for crossing

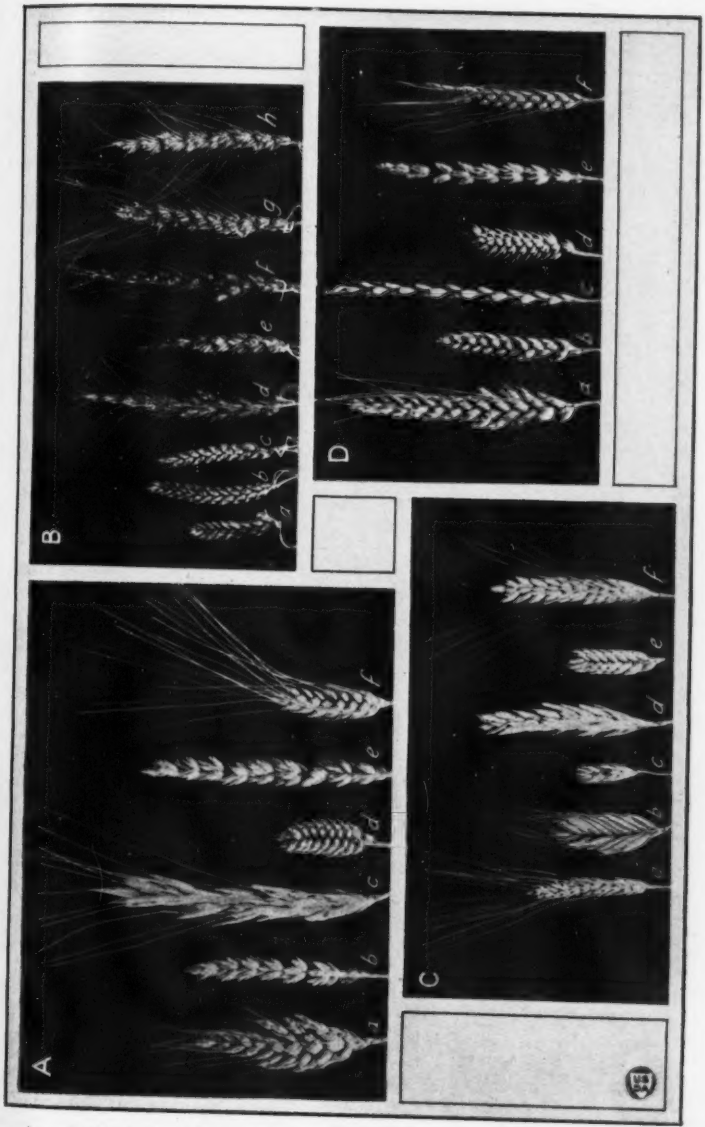
A, *a*.—*Triticum turgidum* (Alaska).
b.—*T. vulgare* (Amby).
c.—*T. plonicum* (Polish).
d.—*T. compactum* (Washington Hybrid 143).
e.—*T. vulgare* (Marquis).
f.—*T. durum* (Kubanka).

Marquis × Alaska F_4

B. *a–h*.—Various types of segregates resulting from the most intermediate types of F_3 segregates. The numbers correspond to the numbers in Table VI, where the description, chromosome number, and sterility of each plant is presented.

D. *a–f*.—Various types of F_2 segregates from the cross Marquis × Alaska. In addition to parental types individuals are recovered which resemble *T. Spelta* and *T. durum*.

C. *a–f*.—Types of segregates from the F_2 of the cross Hybrid 143 × Polish.


B
D
C
A

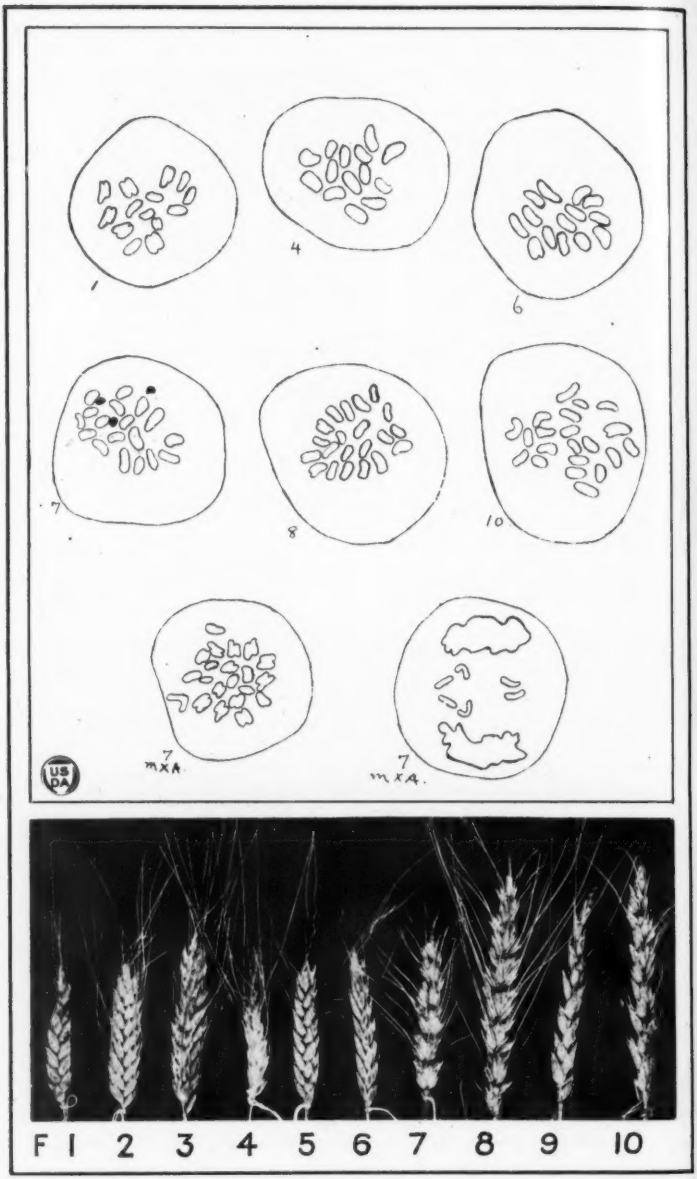

1
4
6
7
8
10
7 mxA
7 mxA
F1 2 3 4 5 6 7 8 9 10

PLATE 2

Figures 1, 4, 6, 7, 8, 10 are from camera lucida drawings of F_4 segregates of Amby × Kubanka and correspond to the numbers of the segregates shown below. These figures are from pollen mother cells at the time of the first reduction division.

Figures numbered 7 (M × A) are from segregate *g* of Marquis × Alaska shown in Plate 1. The side view of the heterotypic division shows the three lagging chromosomes soon after they have divided.

F. 1–10.—Segregates of Amby × Kubanka F_4. The numbers correspond to the chromosomes figures shown above and to the numbers shown in Table VI. The description, chromosome number, and degree of sterility of each of the segregates pictured are shown in Table VI.

DETERMINATION OF TEMPERATURES FATAL TO THE POWDER-POST BEETLE, LYCTUS PLANICOLLIS LECONTE, BY STEAMING INFESTED ASH AND OAK LUMBER IN A KILN[1]

By T. E. SNYDER, *Entomologist*, and R. A. ST. GEORGE, *Assistant Entomologist, Forest Insect Investigations, Bureau of Entomology, United States Department of Agriculture*

INTRODUCTION

Previous preliminary experiments conducted to determine temperatures fatal to Lyctus "powder-post" beetles in the dry kiln have indicated that it is necessary to attain a high temperature for a short period, that is, where the humidity does not reach the saturation point, a temperature of 180° F. must be maintained for at least one-half hour after the ordinary kiln-drying operation.[2] There are objections to subjecting wood to such high temperatures, especially where great structural strength is demanded in its subsequent use, as in the construction of airplanes, for it is likely to weaken the wood fibers as well as to cause discoloration. With these disadvantages in mind, and the knowledge that it is more economical to steam infested lumber in a kiln at a low temperature for a short period than at a high one after the longer period of kiln drying, it was decided to conduct some experiments by subjecting lumber to live steam at lower temperatures for short periods with a saturated atmosphere, to obtain the range of temperatures fatal to the powder-post beetles. Through the courtesy of officers of the United States Navy Department, Bureau of Construction and Repair, and the Naval Aircraft Factory at the navy yard, League Island, Philadelphia, Pa., a series of cooperative experiments along this line was conducted in November and December, 1923, and in January, 1924.[3]

MATERIAL TREATED

The material used in these experiments consisted of infested ash and oak lumber. The former had been piled for nearly 10 years in the open where it was exposed to attack by the southern powder-post beetle, *Lyctus planicollis* Le Conte. The larvæ of this beetle had practically ruined the entire sapwood, rendering it unfit for any use other than fuel. All of the stock was of high-grade material. The ash lumber, being the more seriously damaged and the more infested with insects, was the wood principally used in the experiments.

THE KILN

The kiln used is of the water-spray type and its dimensions are approximately 60 by 14 by 14 feet. Live steam is admitted into it through two pipes, 1¼ inches in diameter, running lengthwise through the center. Along the upper side of these pipes, at intervals of 12 inches, there are holes one-fourth of an inch in

[1] Received for publication Apr. 22, 1924—issued Nov., 1924.

[2] SNYDER, T. E. HIGH TEMPERATURES FOR THE CONTROL OF LYCTUS "POWDER-POST" BEETLES. Jour. Forestry 21: 810-814. 1923.

[3] Special acknowledgment should be made to Capt. G. N. Rock, Bureau of Construction and Repair, Navy Department, Washington, D. C., A. N. Miller, mill foreman, Naval Aircraft Factory, Philadelphia, Pa., and C. C. Shackford, Naval Aircraft Factory, whose hearty cooperation have made these tests possible.

diameter through which the steam is allowed to escape into the kiln for a certain length of time, six hours for every inch of thickness of the lumber being formerly the period of steaming. Then dry heat is applied and the hot air rises through the lumber, cools, and settles toward the bottom of the kiln. The circulation is completed by air currents set in motion by sprays of water coming from jets about 18 inches apart, directed downward, on pipes along the sides of the kiln. These jets of water help to regulate the humidity. After the cool air reaches the bottom it passes through the pipes again where it is brought to a higher temperature.

The temperatures in the following experiments were governed by a Taylor recording thermometer. This was controlled by placing a maximum thermometer in the kiln on the samples undergoing treatment. The relative humidity, as previously stated, was constant at 100. All temperatures were recorded in degrees Fahrenheit.

PREPARATION OF SAMPLES

The infested lumber was placed in a kiln which was kept at a low temperature (100° F.) for several days to determine if the powder-post beetles were still in the wood.[4] An examination of the material at the end of this time showed that it was still well infested. The presence of active larvæ was shown by piles of boring dust, or powderlike frass, found on and about the pieces of lumber (Pl. 1, A).

The samples were prepared by sawing the ash lumber into boards 1 by 12 by 18 inches and into planks 2 by 12 by 18 inches, making a total of 28 pieces of the former and 69 of the latter, and the oak into 4 pieces, each 1¼ by 12 by 18 inches in size. The samples were divided into three lots as follows:

Lot I. Ash, 7 pieces 1 inch thick and 14 pieces 2 inches thick; oak, none.

Lot II. Ash, 12 pieces 1 inch thick and 6 pieces 2 inches thick; oak, 4 pieces 1¼ inches thick.

Lot III. Ash, 9 pieces 1 inch thick and 20 pieces 2 inches thick; oak, none.

These boards 1 and 1¼ inches thick and planks 2 inches thick were subjected to temperatures ranging from 120° to 160° F. and for different lengths of time. On account of the danger of running the thermostat at a temperature above 160° F., the maximum at which it operates, and because previous experiments by C. C. Shackford had proved that this temperature is fatal to the powder-post beetles, no attempt was made to exceed it.

The pieces were marked with their lot numbers and each was given an individual number. The locations of piles of frass on the samples were marked with blue crayon (Pl. 1, A, B). After the wood was removed from the kiln, these places were watched for signs of activity. Lot I was left in the kiln overnight at a higher temperature than that to which the material had been subjected previously. This caused increased activity and additional piles of frass were noted (Pl. 1, A), proving that the samples were more heavily infested than previously indicated by the piles of frass on the outside. The proportion of sapwood and heartwood was also noted, as well as the depth of the larvæ from the nearest surface. C. C. Shackford ran the kiln and assisted R. A. St. George with the work of inspection.

PROCEDURE

Each lot was treated by holding it at a certain temperature for a definite period of time before changing to a higher temperature, and removing pieces at every 10° interval. At least one piece of each lot was examined by chopping into the

[4] Heating the material in this way was necessary because insects are normally inactive at the low temperatures of the fall and winter months.

sample, noting the condition of the larvæ and placing them in vials for future observation. Copper tags (Pl. 1, A, B) furnishing data as to the treatment were placed on the remaining pieces, which were put in a heated kiln for further observation. Photographs were taken of the samples before and after treatment. After the treatment C. C. Shackford examined the material from time to time and noted its condition. A final examination was made four weeks later. These tests were conducted in practically an empty kiln. When the kiln is full of lumber, time should be allowed for all parts of the wood to reach kiln temperature, at which it should be held for the length of time found to be fatal to the insects.

LOT I

Because it had been previously determined that dry heat at 120° F. was not fatal to the powder-post beetle, indicating that a kiln with a saturated atmosphere would require a higher temperature or a longer period of time, no sample pieces in Lot I were removed until after an exposure of one and one-half hours to a temperature of 130° F.

The initial treatment of Lot I was similar to that used in commercial operations for drying lumber. The lot was placed in the kiln at a low temperature, which was gradually raised, and the lumber left in the kiln over night. This was done to make sure that all parts of the samples were at kiln temperature when the temperature of the wood reached the initial point of the experiment. At 3 p. m. December 11 the samples were placed in the kiln at a temperature of 70° F. By 4 p. m. the temperature had been raised to 100° F., where it remained until 3 a. m. December 12. At 8.15 a. m. it reached 110° F. and at 9.40 a. m. 130° F., where it was held for one and one-half hours. Upon removal of the first pieces the temperature was raised 10 degrees and held there for the same length of time, this operation being repeated until the last lot was removed from the kiln at 160° F. The maximum thermometer showed that the indication of the recording thermometer was 4° too low during the work on this lot.

TABLE I.—*Experiments to determine temperatures fatal to Lyctus planicollis by steaming infested ash lumber in a kiln. Lot I*

Sample No.	Size	Temperature and time held		Time held at accumulated temperature starting at 130° F.	Humidity	Proportion of sapwood	Number of piles of frass noted before steaming	Larvæ chopped out immediately after steaming—number and condition	Final examination, Jan. 10, 4 weeks after steaming. Piles of frass noted; larvæ chopped out where results were doubtful [a]
	Inches.	*°F.*	*Hours.*	*Hours.*	*Per cent.*	*Per cent.*			
1	1×12×18..	130	1½	1½	100	25	(b)		No signs of activity.
2	1×12×18..	140	1½	3	100	95	15		Do.
3	1×12×18..	140	1½	3	100	95	(b)	3, darkened	Do.
4	1×12×18..	150	1½	4½	100	90	1		Do.
5	1×12×18..	150	1½	4½	100	95	3	[c]	Do.
6	1×12×18..	160	1½	6	100	100	(b)		Do.
7	1×12×18..	160	1½	6	100	100	(b)		Do.
8	2×12×18..	130	1½	1½	100	25	1	1, white	Do.
9	2×12×18..	130	1½	1½	100	95	15	12, white; 9, darkened.	Do.
10	2×12×18..	140	1½	3	100	20	(b)	[c]	Do.
11	2×12×18..	140	1½	3	100	10	1		Do.
12	2×12×18..	140	1½	3	100	25	3		Do.
13	2×12×18..	140	1½	3	100	20	1		Do.
14	2×12×18..	150	2½	4½	100	25	3	3 larvæ (1 white).	Do.
15	2×12×18..	150	2½	4½	100	15	1		Do.
16	2×12×18..	150	2½	4½	100	15	1		Do.
17	2×12×18..	150	2½	4½	100	20	1		Do.
18	2×12×18..	160	2½	6	100	5	(b)		Do.
19	2×12×18..	160	2½	6	100	5	(b)		Do.
20	2×12×18..	160	2½	6	100	20	7		Do.
21	2×12×18..	160	2½	6	100	10	1	[c]	Do.

[a] Examined by C. C. Shackford December 15, 17, and 21, and January 3; checked by R. A. St. George on final examination.

[b] No piles of frass noted, but all samples infested.

[c] Examined; none found.

An examination of the larvæ chopped out on December 17 showed that they were all apparently dead, although some were still white and soft. The pieces that were tagged and placed in the kiln for future observation were examined December 14 and did not show any signs of larval activity. A final examination of this lot was made January 10, which verified the foregoing preliminary results (Pl. 1, B).

LOT II

Lot II was held for a longer time at every 10° interval than Lot I. It was not deemed necessary to subject any samples to 160° F. The four pieces of oak were included in this lot. All of the samples were placed in the kiln and their temperature raised at once to the initial temperature without previously bringing all parts of the wood to kiln temperature, as was done with Lot I. At 8.30 a. m., December 13, the lot was placed in the kiln at 100° F. From 8.30 to 9 a. m. the temperature advanced to 130°, where it was held for two and one-half hours, or one hour longer than in the case of the previous lot. From 130° onward, pieces were removed at every 10° interval until the temperature reached 150°. The maximum thermometer showed that during the work on Lot II the indication of the recording thermometer was 2° too low.

TABLE II.—*Experiments to determine temperatures fatal to Lyctus planicollis by steaming infested ash and oak lumber in a kiln. Lot II*

Sample No.[a]	Size	Temperature and time held		Time held at accumulated temperature starting at 130° F.	Humidity	Proportion of sapwood	Number of piles of frass noted before steaming	Larvæ chopped out immediately after steaming—number and condition	Final examination, Jan. 10, 4 weeks after steaming. Piles of frass noted; larvæ chopped out where results were doubtful[b]
	Inches.	*° F.*	*Hours.*	*Hours.*	*Per cent.*	*Per cent.*			
1	1×12×18	130	2½	2½	100	25	(c)	----------	No signs of activity.
2	1×12×18	130	2½	2½	100	25	2	----------	Do.
3	1×12×18	130	2½	2½	100	100	(c)	----------	Do.
4	1×12×18	130	2½	2½	100	100	(c)	----------	Do.
5	1×12×18	140	2½	5	100	100	2	3 larvæ (1 white).	Do.
6	1×12×18	140	2½	5	100	100	2	----------	Do.
7	1×12×18	140	2½	5	100	100	2	----------	Do.
8	1×12×18	140	2½	5	100	100	1	----------	Do.
9	1×12×18	150	2½	7½	100	100	1	----------	Do.
10	1×12×18	150	2½	7½	100	100	(c)	----------	Do.
11	1×12×18	150	2½	7½	100	40	1	----------	Do.
12	1×12×18	150	2½	7½	100	100	(c)	----------	Do.
13	2×12×18	130	2½	2½	100	30	2	----------	Do.
14	2×12×18	130	2½	2½	100	30	2	----------	Do.
15	2×12×18	140	2½	5	100	25	3	----------	Do.
16	2×12×18	140	2½	5	100	25	2	----------	Do.
17	2×12×18	150	2½	7½	100	30	2	----------	Do.
18	2×12×18	150	2½	7½	100	10	5	----------	Do.
19	1½×12×18	130	2½	2½	100	3	(c)	----------	Do.
20	1½×12×18	140	2½	5	100	5	(c)	----------	Do.
21	1½×12×18	150	2½	7½	100	3	(c)	----------	Do.
22	1½×12×18	150	2½	7½	100	3	(c)	----------	Do.

[a] Nos. 1–18 are ash; Nos. 19–22 are oak.
[b] Examined by C. C. Shackford December 15, 17, and 21 and January 3; checked by R. A. St. George on final examination.
[c] No piles of frass noted, but all samples infested.

An examination of the larvæ chopped out on December 17 showed that they were all dead, although some were still white and soft. The tagged pieces were examined with those of Lot I and the results were found to be the same. A final examination of this lot on January 10 showed that all the insects had been killed and the damage checked (Pl. 1, B).

LOT III

Lot III was placed in the kiln at 8.30 a. m., December 14, at a temperature of 90° F., which was raised to the initial point, 120° F., by 9 a. m., and held there one-half hour. Pieces were removed at 10° intervals up to 160° F. Samples were taken out at 120° and 160° F., as well as at the intermediate intervals, because samples in Lots I and II subjected to these temperatures apparently did not contain any active larvæ. It was decided to make removals every half hour to determine when the larvæ ceased to be active. The first two removals at 120° and 130° F. probably did not allow the samples to remain in the kiln long enough for all parts of the wood to reach the kiln temperature. The maximum thermometer indicated that the recording thermometer read 5° too low at 120° F., 2° too low at 130° F., 3° too low at 140° F., 2° too low at 150° F., and 1° too low at 160° F.

TABLE III.—*Experiments to determine temperatures fatal to Lyctus planicollis by steaming infested ash lumber in a kiln. Lot III*

Sample No.	Size	Temperature and time held		Time held at accumulated temperature starting at 130° F.	Humidity	Proportion of sapwood	Number of piles of frass noted before steaming	Larvæ chopped out immediately after steaming—number and condition	Final examination, Jan. 10, 4 weeks after steaming. Piles of frass noted; larvæ chopped out where results were doubtful [a]
	Inches.	*°F.*	*Hours.*	*Hours.*	*Per cent.*	*Per cent.*			
1	2×12×18	160	½	2½	100	20	3	.....	No signs of activity.
2	2×12×18	160	½	2½	100	85	(b)	.....	Do.
3	2×12×18	160	½	2½	100	15	1	.....	Do.
4	2×12×18	160	½	2½	100	20	3	.....	Do.
5	2×12×18	150	½	2	100	15	(b)	.....	Do.
6	2×12×18	150	½	2	100	15	3	.....	Do.
7	2×12×18	150	½	2	100	15	2	.....	Do.
8	2×12×18	150	½	2	100	15	2	.....	Do.
9	2×12×18	140	½	1½	100	25	(b)	.....	Do.
10	2×12×18	140	½	1½	100	15	(b)	.....	2 piles of frass noted Dec. 21.[a]
11	2×12×18	140	½	1½	100	20	2	.....	No piles of frass noted Dec. 21; 6 on Jan. 10.[a]
12	2×12×18	140	½	1½	100	15	(b)	.....	No signs of activity.
13	2×12×18	130	½	1	100	15	(b)	.....	Do.
14	2×12×18	130	½	1	100	10	(b)	.....	4 piles of frass noted Jan. 3.[a]
15	2×12×18	130	½	1	100	20	2	.....	5 piles of frass noted Jan. 3.[a]
16	2×12×18	130	½	1	100	20	(b)	Clerid larva alive; white Lyctus.	36 piles of frass noted Dec. 15.[a]
17	2×12×18	120	½	½	100	20	(b)	.....	17 piles of frass noted Dec. 17.[a]
18	2×12×18	120	½	½	100	20	(b)	.....	2 piles of frass noted Dec 21.[a]
19	2×12×18	120	½	½	100	25	1	.....	11 piles of frass noted Dec. 15.[a]
20	2×12×18	120	½	½	100	95	10	2 Lyctus, 1 clerid alive.	34 piles of frass noted Dec. 15.[a]
21	1×12×18	160	½	2½	100	100	5	.....	No signs of activity.
22	1×12×18	160	½	2½	100	15	(b)	.....	Do.
23	1×12×18	150	½	2	100	25	4	.....	Do.
24	1×12×18	150	½	2	100	20	1	.....	Do.
25	1×12×18	140	½	1½	100	15	(b)	.....	Do.
26	1×12×18	140	½	1½	100	15	(b)	.....	Do.
27	1×12×18	130	½	1	100	15	(b)	.....	Do.
28	1×12×18	130	½	1	100	15	(b)	.....	Do.
29	1×12×18	120	½	½	100	5	(b)	.....	4 piles of frass noted Dec. 29.[a]

[a] Reported by C. C. Shackford and checked on final examination by R. A. St. George.
[b] No piles of frass noted, but all samples infested.

An examination of the larvæ chopped out on December 17 showed that temperatures of 120° and 130° F., when held for only one-half hour, were not fatal to the insects. Living larvæ of the powder-post beetle were obtained from these samples. In addition, immature and mature stages of a beneficial insect known to be predacious on the powder-post beetle were also found alive and in considerable numbers. There were not enough present, unfortunately, to exterminate the injurious forms.

A further examination on December 21 verified these results and showed a revival of the larvæ in samples subjected to temperatures varying from 120° to 140° F. when held there for only one-half hour (Pl. 1, A). Other samples in these lots showed that the larvæ were affected and did not recover until January 3.

A final examination was made on January 10, and the above-recorded results verified. Larvæ probably revived in the samples subjected to temperatures up to 140° F. because all parts of the wood had not reached kiln temperature when removed, or, if so, were not held at that temperature long enough to cause the death of the insects. The samples held at 140° F. had an accumulation of temperatures for one and one-half hours.

It will be noted that samples of Lot I were exposed to temperatures gradually raised to 130° F., and were kept at that temperature for 1½ hours. This treatment was fatal to the powder-post beetles because the wood had remained in the kiln over night at temperatures ranging from 100° to 110° F., and all parts of the samples had reached kiln temperature. Under such conditions the subsequent treatment proved fatal to the beetles.

Results obtained from treating Lot II show that placing samples in the kiln, raising the temperature at once to the initial temperature of 130° F., and holding it there for 2½ hours, is effective in killing any powder-post beetles in the wood.

CONCLUSIONS

Results obtained from the foregoing experiments may be briefly summarized as follows:

1. Temperatures below 130° F. are not fatal to the powder-post beetle *Lyctus planicollis* Lec. when the temperature of infested ash and oak lumber is raised to these temperatures in a kiln by the use of live steam and are held there for only one-half hour, if all parts of the wood have not previously been brought to kiln-drying temperature.

2. Temperatures of 130° F. and upward, maintained for 1½ hours, or longer, are fatal to these insects if all parts of the wood infested by them have at the beginning of the exposure to these temperatures been brought to the minimum temperature of 130° F.

3. The standard kiln-drying schedule for ash and oak, to be used for aircraft stock, in a kiln operated by live steam will prove fatal to the powder-post beetle and will check all damage that is being done in any infested material.

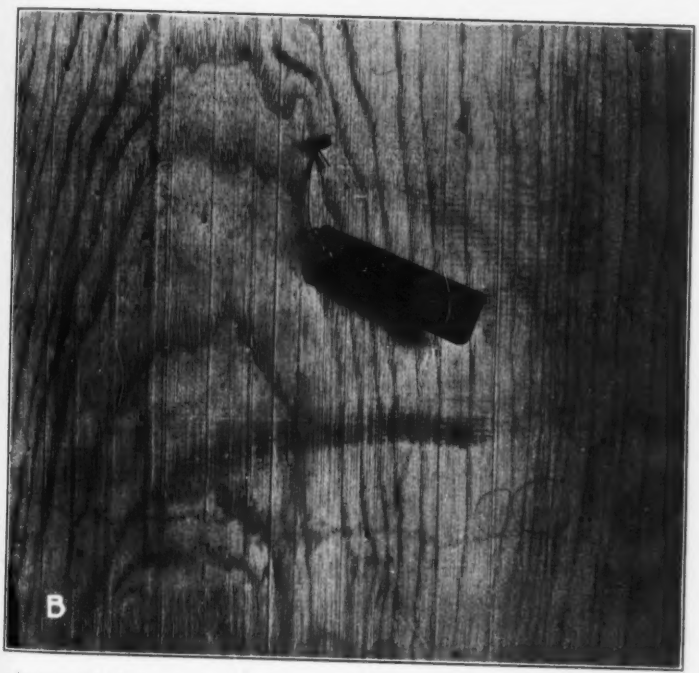
PLATE 1

Lyctus planicollis

A.—Samples of infested wood showing evidences of resumption of larval activity 15 hours after treatment by steaming in a kiln. The wood was held in the kiln one-half hour at a temperature of 120° F. Circles indicate where activity was noted before treatment. (Lot III, Nos. 16 and 20.)

B.—Samples showing absence of resumption of larval activity four weeks after treatment. Held in kiln 2½ hours at a temperature of 130° F. (Lot I, No. 14.)

A


B

By C.
A.
Ind

Evi
an ea
occurr
genic
and in
the w
Bacter

In
near
The
previc
blotch
to the
barley
also b

Isol
to all
inocul
patho
was e

At
the n
seedli
each c
of the
seedli
typica
in sub

At
ducte
transl
with t
oat pl
typica
infecte
from b

The
with t

[1] Rece
cooperat
Seed Co
[2] JONE
CEREALS
[3] SMIT
[4] JONE
11: 625-

BACTERIAL BLIGHT OF RYE [1]

By C. S. REDDY, *Pathologist*, JAMES GODKIN, *formerly Assistant Pathologist, and* A. G. JOHNSON, *Pathologist, Office of Cereal Investigations, Bureau of Plant Industry, United States Department of Agriculture*

Evidently there is more than one bacterial disease of rye (*Secale cereale*). In an earlier publication by Jones, Johnson, and Reddy [2], a bacterial disease of rye, occurring near Madison, Wis., was referred to, the organism of which was pathogenic not only on rye but also on wheat, spelt, and barley. Both in pathogenicity and in cultural characters the organism was very similar to if not identical with the wheat organism which has been described by Smith, Jones, and Reddy [3] as *Bacterium translucens* var. *undulosum* S. J. & R.

In 1921 a bacterial disease of rye was observed by one of the writers (Reddy) near Bloomington, Ill., where it occurred on the leaves of Rosen (winter) rye. The leaf symptoms of the disease at Bloomington were identical with those previously observed on rye in the vicinity of Madison, Wis. In both cases, blotch-like and stripe-like water-soaked lesions (Pl. 1) were noted, very similar to those described by Jones, Johnson, and Reddy [4] for the bacterial blight of barley. The rather conspicuous exudate which occurs on barley and wheat has also been noted on rye.

Isolations made from the Bloomington collections yielded a yellow organism to all appearances identical with the rye organism previously referred to. In inoculations on rye, wheat, barley, and oats this new rye organism proved to be pathogenic only on rye. In all of these inoculation experiments the spray method was employed as previously described for the barley organism.

At Bloomington, Ill., in 1921, two inoculation experiments were conducted with the new rye organism. In both experiments rye and Marquis (spring) wheat seedlings about 4 inches high, growing in rows in the field, were inoculated. In each case an ample number of plants were left uninoculated as controls. In both of these experiments typical bacterial lesions resulted on the rye, while the wheat seedlings and all of the controls remained free from bacterial infection. The typical rye organism was recovered from the rye lesions, and it proved pathogenic in subsequent inoculation experiments.

At Madison, Wis., in 1921 and 1922, two inoculation experiments were conducted. In each, both the new rye organism and the barley organism, *Bacterium translucens*, were used as inocula. In both experiments, parallel inoculations with the two organisms were made in the greenhouse on rye, wheat, barley, and oat plants about 4 inches high. In both series the new rye organism produced typical bacterial lesions only on rye and the barley organism, *B. translucens*, infected only barley as usual. All the uninoculated control plants remained free from bacterial infection.

The morphological characters of the new rye organism were found to be identical with those of *Bacterium translucens* as described by Jones, Johnson, and Reddy.[4]

[1] Received for publication April 19, 1924—issued Nov., 1924. These investigations were conducted in cooperation with the Wisconsin Agricultural Experiment Station, Madison, Wis., and the Funk Bros. Seed Co., Bloomington Ill.

[2] JONES, L. R., JOHNSON, A. G., and REDDY, C. S. BACTERIAL BLIGHTS OF BARLEY AND CERTAIN OTHER CEREALS. Science 44: 432–433, 1916.

[3] SMITH, E. F., JONES, L. R., and REDDY, C. S. THE BLACK CHAFF OF WHEAT. Science 50: 48, 1919.

[4] JONES, L. R., JOHNSON, A. G., and REDDY, C. S. BACTERIAL BLIGHT OF BARLEY. Jour. Agr. Research 11: 625–644, illus. 1917.

The cultural characters were studied in direct comparison with those of *Bacterium translucens*, that is, the two organisms were run in parallel series. In all of these studies of cultural characters the two organisms were found to be identical. The results were the same as given for the barley organism, *B. translucens*, except in one detail as follows: In the case of action on starch, it was previously reported for the barley organism, *B. translucens*, that there was "no evidence of diastatic action on potato starch * * *." In the present investigations, using the more delicate methods described by Conn et al.,[5] it was found that both the barley organisms, *B. translucens*, and the new rye organism produced a very feeble diastatic action on starch noticeable for approximately half an hour after the iodin solution had been applied. After that time it was difficult to detect any halo about the colonies. There was possibly a slight dextrine reaction.

In addition, certain special studies were made on indicator media. Saccharine media containing brom cresol purple and cresol red, respectively, were prepared according to the recommendations of Conn et al.[5]

The new rye organism and the barley organism, *Bacterium translucens*, were used in parallel series. Eight agar slants of each medium were inoculated with each organism respectively, and four slants of each medium were left uninoculated. Both organisms changed the color of each medium to the same degree in the same length of time. Alkaline reactions were produced in all of these media as follows: Pronounced in those containing lactose, maltose, mannit, or glycerine; less pronounced in those containing dextrose; and still less pronounced in those containing saccharose.

On the basis of these studies it is evident that the new rye organism is identical with *B. translucens* and the previously described variety, *B. translucens undulosum*, both in morphological characters and in physiological characters in artificial culture media but differs from both in pathogenicity. Hence, the new rye organism is here designated a new variety of *B. translucens* as follows:

Bacterium translucens secalis n. var.

In morphology and in artificial culture this variety is identical with *Bacterium translucens* and *B. translucens undulosum*.

Bacterium translucens infects only barley.

Bacterium translucens undulosum infects wheat, barley, rye, and spelt.

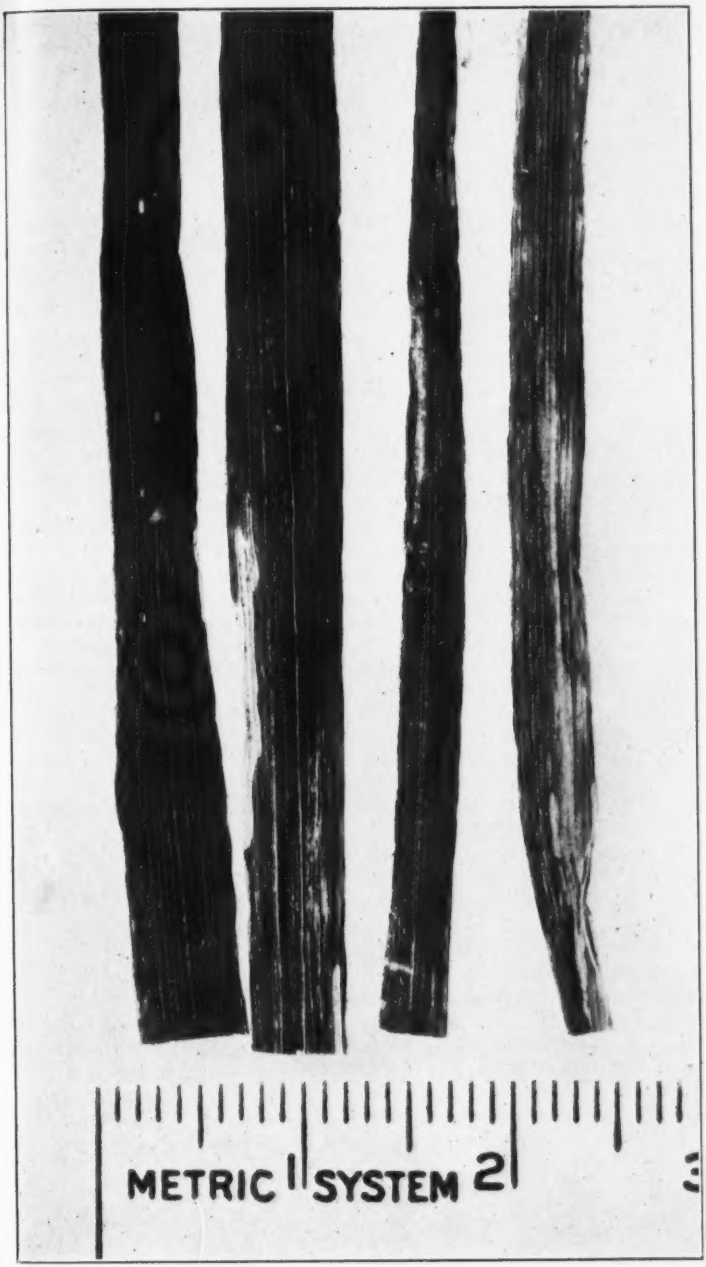
Bacterium translucens secalis infects only rye.

Type locality: Bloomington, Ill.

[5] CONN, H. J., and others. REPORT OF THE COMMITTEE ON THE DESCRIPTIVE CHART FOR 1919. Jour. Bact. 5: 127–143; 315–319. 1920.

PLATE 1.

Bacterial lesions from natural infections on leaf-blades of rye. Specimens collected near Bloomington, Ill., in 1921.


METRIC 1 SYSTEM 2

NON-INHERITANCE OF TERMINAL BUD ABORTION IN PIMA COTTON[1]

By THOMAS H. KEARNEY

Physiologist in Charge, Alkali and Drought Resistant Plant Investigations, Bureau of Plant Industry, United States Department of Agriculture

The normal development of the cotton plant is often interfered with, and various types of malformation result. One of the most common and characteristic of these teratological states is associated with arrested development or abortion of the terminal bud of the axis. The frequency of this phenomenon is indicated by the fact that of 1,109 plants of Pima cotton under observation in 1918, 44, or approximately 4 per cent, had the terminal bud aborted. In a majority of cases the injury occurs during the seedling stage, 35 of the 44 individuals having shown abortion at the time the cotton was thinned. Yet the terminal bud may be lost at any time during the growth of the plant. An individual in which the injury occurred at a comparatively late stage of development is shown in Plate 1, with an adjacent, uninjured plant for comparison.

The cause of abortion of the terminal bud is not known, although the injury is frequently associated with leaf-cut or tomosis,[2] and indications of injury by the larvae of an insect were observed in one case. If it occurs early in the life of the plant, one of the vegetative branches produced at low nodes of the axis may assume an erect position, simulating so closely a true axis that close observation is required to determine that the original growing point has been destroyed or arrested. If abortion takes place in a later stage of development, as in the individual shown in Plate 1, the fruiting branches just below the point of injury become elongated and often branched, with a tendency to assume a more nearly erect position and to produce abnormally large leaves of coarse texture. The same phenomenon may be induced by artificially "topping" the plant.

As in all such cases, it is important to know whether we are dealing with a heritable character. If this malformation is inherited, aborted individuals should be removed in roguing seed-increase fields, for they are nearly always less fruitful than normal plants. In an endeavor to solve this problem, 12 aborted individuals of the Pima variety of Egyptian cotton, as well as 12 normal individuals to serve as controls, were selected at the United States Field Station, Sacaton, Ariz. The control for each aborted plant was either the next plant in the row or the nearest normal plant that could be found. Each aborted plant and its control were given the same number. Flowers on all of the aborted and normal individuals were bagged to prevent cross-pollination and from the resulting self-fertilized seed progenies of the 24 plants were grown the following year. Each pair of progenies representing a normal and an aborted plant were located in the same portion of the field, so as to reduce to a minimum the influence of soil heterogeneity.

[1] Received for publication April 9, 1924—issued Nov., 1924.

[2] COOK, O. F. LEAF-CUT, OR TOMOSIS, A DISORDER OF COTTON SEEDLINGS. U. S. Dept. Agr. Bur. Plant Indus. Circ. 120: 29-34, illus. 1913.

Table I gives for each progeny the total number of plants before thinning, and the number and percentage of individuals of which the terminal bud was aborted at some stage of development. The data also are combined for all progenies of aborted individuals and all progenies of normal individuals, taken as one array in each case.

TABLE I.—*Numbers and percentages of aborted plants in progenies of aborted and normal individuals of Pima cotton*

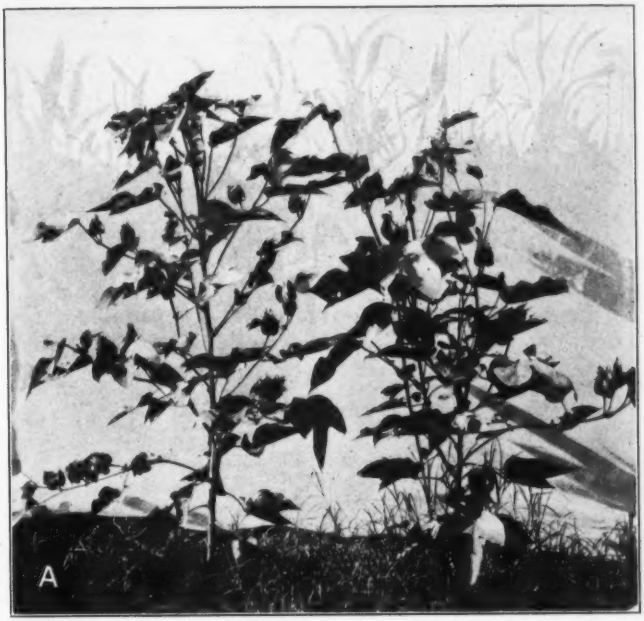
Progeny of plant No.	Progenies of aborted plants			Progeny of plant No.	Progenies of normal plants		
	Total individuals	Number aborted	Percentage aborted		Total individuals	Number aborted	Percentage aborted
1	43	2	4.6	1	37	6	16.2
2	34	1	2.9	2	43	5	11.6
3	44	2	4.5	3	48	2	4.2
4	38	2	5.3	4	43	1	2.3
5	47	1	2.1	5	53	1	1.9
6	49	3	6.1	6	45	1	2.2
7	55	0	0	7	65	4	6.2
8	49	1	2.0	8	41	3	7.3
9	39	1	2.6	9	50	0	0
10	35	2	5.7	10	51	1	2.0
11	61	0	0	11	45	0	0
12	46	3	6.5	12	48	2	4.2
Total	540	18	3.33±0.52	Total	569	26	4.56±.009

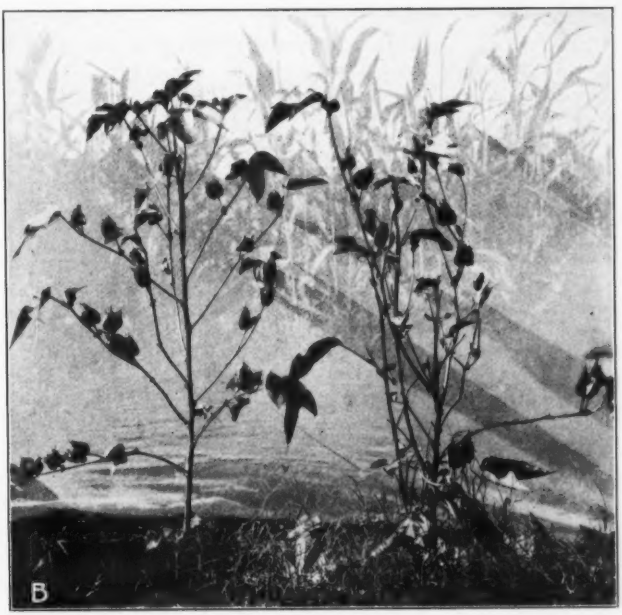
When all progenies of aborted and of normal plants, respectively, are considered as one array, the latter give a slightly higher percentage of aborted individuals, but the difference is not significant, being only 1.6 times its probable error. It is concluded that abortion of the terminal bud in this material is not an inherited character.

PLATE 1

A.—At the right, a plant of Pima cotton with terminal bud of the main stalk aborted; at the left, a normal plant in which the development of the axis has not been interrupted.

B.—The same plants with most of the leaves removed.


A


B

RE
P
G

By
P
of

D
that
alth
stru
pera
Stat
to w
hand
Carc
obta
on t
with
cont

A
spec
pera
kille
expo

U
resis
pera
of t
temp

W
kille
rang
in 3
The
activ
after

W
kille
as lo
8 da
but
temp

W
kille
men
ture

[1] Re

Journ
Wash

RELATIVE RESISTANCE OF THE RICE WEEVIL, SITOPHILUS ORYZA L., AND THE GRANARY WEEVIL, S. GRANARIUS L., TO HIGH AND LOW TEMPERATURES[1]

By E. A. Back, *Entomologist in Charge*, and R. T. Cotton, *Entomologist, Stored Product Insect Investigations, Bureau of Entomology, United States Department of Agriculture*

During several years of study on the grain weevils the writers have observed that the rice weevil, *Sitophilus oryza L.*, and the granary weevil, *S. granarius L.*, although belonging to the same genus and closely resembling each other in size, structure, and habits, differ markedly in their resistance to high and low temperatures. Whereas the rice weevil is predominant in the Middle and Southern States, it has not established itself in the extreme Northern States and is unable to withstand the northern winters except in protected situations. On the other hand, the granary weevil is seldom if ever found in the South below North Carolina, but is the predominant form in the Northern States. In order to obtain more precise information on the relative effects of various temperatures on the two weevils, a number of experiments were carried on in the laboratory with small refrigerator units and incubators, in which the temperatures could be controlled. The results obtained were striking and seemed worthy of record.

A constant temperature of zero Fahrenheit proved quickly fatal to both species, although the granary weevil was able to withstand even this low temperature slightly longer than the rice weevil. Adults of the rice weevil were killed after an exposure of four hours, and adults of the granary weevil after an exposure of five hours, to this temperature.

Up to a certain point, as the temperature was increased, the difference in resistance between the two species became more and more apparent. At a temperature of 5° F. an exposure of four and a half hours was sufficient to kill adults of the rice weevil, whereas an exposure of seven and a half hours at the same temperature was required to kill adults of the granary weevil.

With a temperature ranging from 15° to 20° F., adults of the rice weevil were killed in 3 days and adults of the granary weevil in 14 days. With a temperature ranging from 20° to 25° F. a majority of adults of the rice weevil were killed in 3 days, although a few showed feeble movements after an exposure of 6 days. These longer-lived individuals all died shortly thereafter, without regaining normal activity. Adults of the granary weevil were killed at this temperature only after an exposure of 33 days.

With a temperature ranging from 25° to 30° F., adults of the rice weevil were killed in 8 days and adults of the granary weevil in 46 days, or nearly six times as long. At 30° to 35° F. a majority of adults of the rice weevil were killed in 8 days; a few, however, showed faint movements after an exposure of 16 days, but died without regaining normal activity. An exposure of 73 days at this temperature was necessary to kill adults of the granary weevil.

With a temperature ranging from 35° to 40° F., adults of the rice weevil were killed in 18 days. A few specimens of the granary weevil showed faint movements after being exposed to this temperature for 111 days. With a temperature ranging from 40° to 45° F. adults of the rice weevil were killed in 80 days,

[1] Received for publication Apr. 19, 1924—issued Nov., 1924.

this slight increase in temperature associating itself with a marked increase in longevity. Specimens of the granary weevil were still alive after an exposure to this temperature for 105 days.

With a temperature ranging from 50° to 60° F., and under the other conditions prevailing, the normal lives of both species of weevil were greatly prolonged. Adults of the rice weevil confined in a refrigerator with this range of temperature lived for a period of 558 days, and specimens of the granary weevil in the same refrigerator for a period of 873 days. The normal life of the rice weevil in summer is from 100 to 200 days, while that of the granary weevil averages from 200 to 250 days.

The immature stages of these two weevils show a similar difference in their powers of resistance to low temperatures. Eggs of the rice weevil perished after being exposed to a constant temperature of 30° F. for 4 days, whereas eggs of the granary weevil survived an exposure to the same temperature for a period of 28 days. Larvæ of the rice weevil were killed by an exposure to a temperature of 30° F. for a period of 11 days, while larvæ of the granary weevil survived an exposure of 44 days to that temperature.

The data previously quoted have been derived from experiments with several thousand individuals. However, the susceptibility to low temperatures varies so much in individuals of the same species that very large numbers must be experimented with in order to arrive at definite conclusions regarding the lethal qualities of any one temperature. The foregoing figures can not be considered quite final until further experiments involving many more individuals have been completed. More detailed results regarding the lethal effect of various low temperatures on the different stages of these two weevils will be published later, when experiments now under way have been completed.

The effect of high temperatures on the two weevils is also of interest, although there are no very great differences in the reactions of the two species to heat. With both species constant temperatures above 95° F. soon prove fatal. Of a large number of adults of the rice weevil confined in an incubator at a temperature ranging from 95° to 98° F., all were killed at the end of 9 days. Adults of the granary weevil confined in the same incubator were all dead at the end of 13 days. A temperature of 120° F. killed adults of both species in three hours, and a temperature of 130° F. within 30 minutes. It is interesting to note that oviposition ceased at a constant temperature of 94° F.

UNINUCLEATED AECIDIOSPORES IN CAEOMA NITENS, AND ASSOCIATED PHENOMENA[1]

By B. O. DODGE

Pathologist, Fruit-Disease Investigations, Bureau of Plant Industry, United States Department of Agriculture

INTRODUCTION

The cytology of the mallow rust *Puccinia malvacearum* has been studied by Werth and Ludwigs (*15*), Moreau (*12*), and others.[2] Nothing was discovered that suggested to these investigators that the omission of the spermogonial structures has any special significance whatever in the life of the rust. The discussions and controversies in regard to this short-cycled Puccinia have largely centered around questions as to time and method of infection and of over-wintering. Cell fusions take place in the sorus, each binucleated cell of the teleutospore becomes uninucleated by nuclear fusion, divisions occur and a 4-spored promycelium is developed.

In describing the spore forms of species of rusts mycologists frequently state that spermogonia (pycnia) are unknown or wanting. A preliminary study of the short-cycled orange-rust, *Caeoma nitens*, on blackberries, has led the writer to suspect that the suppression of spermogonia in the life of this rust may follow as the result of something more fundamental than that which leads to the omission of the pycnidial stage by some species of the ascomycetes. In other words, if the facts can be interpreted in the light of phylogenetic developments, it may be discovered that the omission or suppression of the spermogonial stage is in reality of sexual significance although the spermatia in themselves take no part in a process of fertilization. A brief résumé of the occurrences which led the writer to give closer attention to the cytological details in the growth of the orange-rust of Rubus may perhaps serve as a statement of the main features presented in this paper.

Several years ago while growing rusts in the greenhouse for class use at Columbia University, the writer observed that in certain cases of infection of blackberry by the short-cycled orange-rust, no spermogonia were developed on plants whose leaves were maturing the aecidial stage. This was in striking contrast with what is commonly known to occur. One of the most familiar sights in this country is the appearance of etiolated blackberry shoots whose leaves are covered with spermogonia when the infected sprouts emerge from the ground some days in advance of the others. In reporting on the results of work relating to infection of blackberries with the "haploid" generation of the orange-rusts (*3*), it was pointed out that as the inoculated plants of the Iceberg variety began to show signs of infection, no spermogonia could be found, even though the shoots were several inches high and the young aecidia were beginning to develop. That this omission of the spermogonial stage was not due specifically to peculiarities of this host, which is

[1] Received for publication June 30, 1924—issued Nov., 1924.

[2] Reference is made by number (italic) to "Literature cited," p. 1058.

an albino variety, was evident later when plants of the Mercereau variety similarly infected also failed to show spermogonia. Infected plants of both varieties were observed again the following year to see if spermogonia might not develop the second year after infection. At no time in the past three years has the rust on these plants produced spermogonia. This fact was the more interesting because on those plants of the Ancient Briton and Eldorado varieties which had been infected with the short-cycled rust in one of the experiments, spermogonia had always preceded the aecidia. The rust on a Taylor blackberry which was infected when received from the nursery, developed both spermogonia and aecidia, but the rust on other plants of this variety which later were artificially infected did not develop spermogonia.

During the spring of 1923, two root shoots of the Iceberg variety were inoculated with orange-rust, the one was infected by sowing sporidia from aecidiospores of the strain from the Ancient Briton which had developed spermogonia, the other Iceberg was infected with spores from rust on wild blackberry. Both plants inoculated became systemically infected and developed aecidia in 1924. The first plant showed many spermogonia on the leaves from the basal shoots as soon as they developed; the infected basal shoots from the other plant developed only aecidia, no spermogonia. While endeavoring to account for the occasional suppression of the spermogonial stage of the short-cycled orange-rust, it was discovered that aecidiospores of those strains of the rust omitting the spermogonial stage are uninucleated. Cell fusions do not regularly take place in the aecidium primordium. The uninucleated spores develop promycelia when they germinate but the promycelia are 2-celled, and each cell produces only one sporidium.

As the figures to be discussed later show, the number of cells in a promycelium is not constant for any strain. Promycelia are reported as 2-celled, or 4-celled, when one sees large numbers that are 2-celled or 4-celled, as the case may be. If no spermogonia could be distinguished with a hand lens on an infected leaf it would be reported as without spermogonia, when a more careful examination with a higher-powered microscope might prove that poorly developed or vestigial spermogonia were present. In the discussion which follows, the statement as to absence of spermogonia should be read with this understanding.

The absence of spermogonia may seem to be a point particularly stressed in the following account, when it is clear that the facts regarding the production of 2-celled promycelia which function is the feature which is being set forth as a new departure from the regular order of promycelia in the rusts. It will be shown later, however, that both of these features are merely the outward expression of something of relatively far greater significance fundamentally, and that is, that an aecidium of the orange-rust of Rubus may arise without cell fusions and that the spores matured without such cell fusions are generally uninucleated.

Since the long-cycled, as well as the short-cycled orange-rusts, have both been proved to be widely distributed in America on a number of species of Rubus, further evidence on the mere question of their distribution in the form of extensive tables showing germination tests is unnecessary, except as some new element enters the discussion. The discovery of uninucleated strains with 2-celled promycelia makes it highly desirable that further germination tests be made in such a way as to record the different types of promycelia as correlated with the relative abundance of spermogonia, as well as the size, form, and color of the spores. The abundance of the strain which develops 2-celled promycelia may be judged from the following accounts of collections gathered at random in various localities in one season.

OCCURRENCE OF CAEOMA NITENS WITHOUT SPERMOGONIA

Miss Ruth Colvin, who was assisting the writer with this work, made one collection of orange-rust about every mile from wild blackberries May 24 along the road between Washington and Fairfax, Va. The results of her germination tests show that only 11 of the 30 collections were of the strain whose spores develop 2-celled promycelia; only one long-cycled specimen was obtained, in this case the host happened to be the black raspberry, *Rubus occidentalis*. In most regions around Washington one would certainly find on such a trip blackberries infected with the long-cycled form.

Miscellaneous gatherings on wild blackberries near Upper Marlboro, Md., always contain some specimens which are long-cycled. Twenty-two specimens were gathered from wild blackberries in this region June 2. The presence or absence of spermogonia was determined in the field by Prof. R. A. Harper and Dr. C. L. Shear. Of the 22 gatherings, seven happened to be long-cycled; the spores from the eight specimens without spermogonia produced 2-celled promycelia, and those from three gatherings developed only 4-celled promycelia. The rust on three different plants was of the type which develops spores of two sorts; some produce long germ tubes characteristic of the long-cycled forms, others germinate with 4-celled promycelia. The specimens which were proved to be of the long-cycled type were also characterized by the greater abundance of spermogonia.

The results of germination test of specimens collected May 9 at Chadbourn, N. C., and May 10 to 12 at Louisville and Vidalia, Ga., are such as to suggest that the strain which does not develop spermogonia normally and whose spores form 2-celled promycelia, greatly predominates in the South. The specimens tested, however, were gathered within a limited area in each place, so that a further survey would be necessary in order to determine this point. Of the 18 specimens tested only one was found which developed 4-celled promycelia. This was found on *Rubus trivialis* at Louisville, Ga.

Miss Colvin sent in 11 specimens gathered May 30, between Washington, D. C., and Gettysburg, Pa. No spermogonia could be found on leaves of six specimens whose spores developed 2-celled promycelia. Spermogonia were abundant on four different specimens, three of which were short-cycled and formed 4-celled promycelia. The other one was long-cycled. One specimen showed a few spermogonia and some 4-celled promycelia were found in the culture but 2-celled promycelia were much more abundant. A few other cases of infection found elsewhere have proved to be of a type where 2-celled promycelia are developed, although spermogonia are present on the leaves.

On June 3, 19 collections were obtained at the experimental farm at Bell, Md. Leaves on nine infected plants showed spermogonia and the rust was of the 4-celled promycelium type in six cases; the other three gatherings were long-cycled. Spores from nine specimens showing no spermogonia developed 2-celled promycelia. One large plant with a number of canes was clearly infected with two different strains of orange-rust. Leaves on most of the canes showed an abundance of spermogonia. Here the rust was long-cycled. No spermogonia could be found on leaves on one cane and here the rust was short-cycled, the promycelia being 2-celled (see Pl. 5, B, D).

On June 12, Professor Harper and Dr. F. D. Fromme sent in nine specimens from rusted blackberries gathered on the road to Mountain Lake, Va. No spermogonia could be found on the three specimens whose spores germinated with 2-celled promycelia. Five specimens showed an abundance of spermogonia. Only one of this number proved to be short-cycled, 4-celled promycelia being formed as the spores germinated.

96461—24†——6

Dr. N. E. Stevens, while en route by automobile from Washington, D. C., to Providence, R. I., June 4 to 6, sent in 35 specimens of orange-rust on blackberries and dewberries. The germination tests show that the strain which develops spermogonia and 4-celled promycelia was more abundant along this route at that time than was the strain without spermogonia and producing 2-celled promycelia; only 7 specimens were of the latter type, while 23 were of the type which develops 4-celled promycelia.

Whether the strain which develops 2-spored promycelia may not be relatively more abundant as one goes farther South can not be said with certainty. When the result of germination tests of rust collected from northern New Jersey and central New York are compared with those from North Carolina and Georgia, it might seem that the strain without spermogonia which develops 2-celled promycelia is more abundant in the South. All of the specimens collected at Junius, Geneva, and Albany, N. Y., June 16 to 18, showed at least some spermogonia. Only a few localities were visited but it is possible that the strain in which the spermogonial structures are poorly developed or omitted is not so common in the North. Of the 24 specimens tested 5 were long-cycled. Two-celled promycelia developed from spores from 2 specimens.

Several other collections were made at Ridgewood, N. J. Owing to the excessively hot weather prevailing and the delay in the mails, very poor germination was obtained. All of these specimens collected June 19 on wild dewberry showed spermogonia when carefully examined later. When germination was such as to enable one to determine the nature of the promycelium, it was found to be 4-celled. A few long germ tubes were seen in cultures from 6 specimens on blackberry. Very likely this rust was long-cycled and further search later will result in the discovery of telia in this vicinity.

All of the leaves in specimens collected at Wells Beach, Me., June 22, on wild dewberry and blackberry, were covered with spermogonia. Tests proved that the rust here is long-cycled. Dr. D. Folsom has sent in specimens of orange-rust collected in Maine. Germination was tested at Orono and the rust found to be short-cycled.

A number of plants of different varieties and species of Rubus infected with orange-rust are grown in the greenhouse at Arlington, Va., from year to year. In every case here so far tested, where spermogonia are readily seen with a hand lens, the rust is either long-cycled, or if short-cycled, it develops 4-celled promycelia.

With the results of all the germination tests reported above in mind, it is possible to make three general statements covering this phase of the question.

(1) Spermogonia are always found in considerable numbers on leaves of Rubus infected with the long-cycled orange-rust *Gymnoconia interstitialis*.

(2) If no spermogonia are present on a leaf showing aecidia of orange-rust the spores will be found to be uninucleated, and on germination they will form 2-celled promycelia.

(3) In strains of the short-cycled rust whose spores develop 4-celled promycelia, spermogonia always precede or accompany the formation of aecidia.

TWO-CELLED PROMYCELIA FROM A STRAIN HAVING SPERMOGONIA

During the prosecution of this survey work there has been found very rarely a form of orange-rust in which spermogonia appear to be fairly well developed, yet the æcidiospores are uninucleated and develop 2-celled promycelia. A Crandall blackberry was found infected with this type. Some of the Eldorado blackberries in Doctor Rankin's experimental plots at Geneva, N. Y., show

spermogonia. A few 2-celled promycelia were seen in cultures from this collection. A blackberry from Doctor White's plot at the Arlington Experiment Farm in Virginia regularly shows rust with spermogonia, yet practically every spore produces a 2-celled promycelium. Sections show that the spores are mostly uninucleated. One other specimen sent in appears to be of the same nature. So far as has been learned, every specimen of this interesting form occurred on a cultivated variety of blackberry. It is the only form with spermogonia so far studied that has uninucleated æcidiospores.

CHARACTERISTIC FEATURES OF PROMYCELIA OF THE SHORT-CYCLED ORANGE-RUST

In the preceding discussion, in order to avoid confusion, no mention has been made of the great variability which may sometimes occur in the form and size of the promycelia which develop when spores from a single æcidium are germinated. Likewise, the promycelia were said to be 2-celled or 4-celled, as the case might be, disregarding the fact that in certain germination tests promycelia with from 3 to 8 cells were found. Furthermore, the number of cells which a promycelium develops does not necessarily correspond to the number of nuclei visible or to the number of sporidia that finally mature. Various types of promycelia, as they appeared in the germination test cultures, will be described. The method of origin of the chains of æcidiospores and the behavior of the nuclei during germination and formation of sporidia will then be considered.

As a rule, the æcidiospores of the strain which seems to omit the spermogonial stage are smaller than those of the long-cycled form. The color characters of the æcidia are not always dependable, but, in general, when the aecidia are rather light yellowish-orange as contrasted with reddish-orange colored (Pl. 5, B, D) the spores will be found smaller, and less uniform in shape and size. These small spores are the ones that regularly produce 2-celled promycelia on germination. The more common types of this promycelium are shown in Plate 1, A to I.[1] Two septa are usually plainly visible, cutting off two cells, leaving the spore and a short piece of the germ-tube without cytoplasmic contents. The promycelia are rather slender and their sporidia are not large. As compared with these structures developing from the large spores matured by other short-cycled strains, they are certainly smaller. In cultures of germinating spores from plant No. 497 no promycelia were found with four sporidia attached. Plate 1, H, shows three sporidia on a 2-celled promycelium which is rather "abnormal". Sometimes by following this type of growth a little further, one will find that the contents of one of the sporidia will disappear so that only two finally are discharged. The sterigmata are frequently long and filamentous (Pl. 1, D). This seems to be due to the conditions under which the spores germinate. Normal sporidia are finally developed.

The more common types (4-celled) of promycelia developed from spores of strains producing spermogonia are shown in Plate 1, J to M. These are 4-celled and will all develop four sporidia.

Certain odd types are also figured. They are, however, perfectly normal. A 9-celled promycelium is shown in Plate 1, N. Some of the cells are dead or empty but six sporidia are being matured. Forked promycelia are not very rare. Figure R shows one with eight cells, six of them alive; one sporidium has been discharged, two more are matured, and one is just forming.

The influence that the conditions attendant on spore germination have on the form of the promycelia is occasionally very astonishing. For example, the spores from plant No. 569 develop in the warm laboratory very long germ

[1] The 4-mm. dry lens was used in drawing the figures in Plate 1; the 1.5-mm. oil immersion lens for Plates 2 to 4, inclusive.

tubes (Pl. 1, V), resembling those of the long-cycled Gymnoconia. They become 4-celled, however, and mature four sporidia. Plate 1, S, shows such a promycelium as it would appear a little later. Five-celled promycelia (Pl. 1, T) with one sporidium from each, are sometimes seen in cultures. The formation of five cells and five nuclei after a reduction division is not the regular order of procedure as commonly understood. These odd types of germination are referred to in order to focus attention on the question of nuclear behavior during and after aecidiospore formation, and to raise the question as to whether or not nuclear fusions followed by reduction divisions are always to be found in the short-cycled orange-rusts.

While every specimen of the rust so far discovered which omits its spermogonial stage is characterized by 2-celled promycelia, as previously noted, there are certainly clear-cut cases where spores from leaves with spermogonia are uninucleated and develop 2-celled promycelia with only two sporidia (Pl. 1, W).

ORIGIN OF AECIDIA WITH BINUCLEATED AECIDIOSPORES

In the light of what is known of the vagaries of Rubus orange-rusts, it is impossible to say what was the nature of the material which Olive (*13*) used as the basis for his cytological work on the orange-rust. It was gathered in Indiana on Rubus sp. He figures the Christman cell fusions referred to as "sexual fusions." The rust that Olive studied evidently conformed in every way to what might be expected of the long-cycled form Gymnoconia.

Kunkel (*5*) presumably did not find anything in his studies of the development of the aecidial sorus of the short-cycled form of the orange-rust to suggest that there might be at times some departure from the regular order of procedure in the growth of the aecidium. According to him the two nuclei originally found in the aecidiospore fuse before germination of the spore and as the germ tube begins to push out the fusion nucleus divides, sometimes while yet in the spore; the first division may also occur in the promycelium. After the second division the cross walls are laid down so that four uninucleated cells comprise the mature promycelium. Each of the four cells then develops a sporidium containing a single nucleus. In the manner of their origin, in the behavior of their nuclei on germination, and in the type of promycelia formed from them, the aecidiospores of *Caeoma nitens* were thus, according to Kunkel, not unlike those of *Endophyllum sempervivi* as reported by Hoffman (*4*) and others.

The writer's studies have been confined to preparations made from material obtained from plants infected with rust whose spores have been germinated.

There are many interesting features in the development of aecidia which need further attention other than the so-called "sexual fusions," but as the question relating to the ultimate form of the promycelium is in the main determined at the origin of the aecidiospore, it will be necessary to give this phase of the subject some attention. Disregarding what occurs when the aecidia of the long-cycled orange-rust are formed (Pl. 2, T), the origin of the chains of spores in those strains where 4-celled promycelia are regularly developed from aecidiospores will first be referred to. Cell fusions (Pl. 2, M to S) in numbers can be found in sections of aecidial primordia of the rust on an Iceberg blackberry No. 543. Spermogonia were developed in large numbers on this plant and germination tests showed that most of the spores germinated as short-cycled, forming quite regularly 4-celled promycelia. Binucleated spores and intercalary cells are cut off in regular order above the fusion cells.

In no case is there any indication in these sections of a fusion of the two nuclei in a spore. Hoffman (*4*) shows that in *Endophyllum sempervivi* the two nuclei

fuse and then often undergo the first division before the spore is shed. The writer's sections of telia of the long-cycled form Gymnoconia show that the two nuclei fuse as the teleutospore reaches maturity. Is it possible that the two nuclei of the short-cycled orange-rust spore never fuse? If so, the reduction division would be omitted, only that standing in place of the homoeotypic division persisting to give the four nuclei of the "normal" promycelium.

In some preparations from an infected loganberry "two-legged" cells are very difficult to find (Pl. 2, L). Very likely such figures represent sections at right angles to the pairing cells so that only one of the "leg" cells appears in the section. It is not impossible that chains of binucleated spores may sometimes, or even regularly, arise by mere nuclear division as claimed by Kursanov (*8*). It is certainly strange that fusion cells are so hard to find in this strain on loganberry.

Rust from a blackberry also shows aecidial chains of 2-nucleated spores (Pl. 2, I, J) where it is also difficult to understand why more examples of two-legged fusion cells are not to be found. The cytology of this form of the orange-rust is being given further attention.

ORIGIN OF SORI WITH CHAINS OF UNINUCLEATED AECIDIOSPORES

There being no question as to the existence of cell fusions, at least in the aecidium primordium of the Gymnoconia orange-rust, the form of rust on blackberry which omits the spermogonial stage will next be considered.

Plate 2, A, represents merely in outline and position the structures in an aecidial sorus of the rust on Crandall blackberry which was obtained May 17, 1922. The uninucleated basal cells arise from uninucleated cells of the sorus primordium. Intercalary cells are cut off and the spores are matured in a normal fashion. There were no cell fusions in this sorus. At B a chain of 2-nucleated spores and interstitial cells is shown adjacent to chains of uninucleated spores. Kursanov (*6*) says, in effect, that in *Aecidium leucospermum* this would mean that the nucleus of the original basal cell simply divided and thereafter 2-nucleated cells are cut off. In Plate 2, D and F, are shown chains of spores in an aecidium from plant No. 497, most of whose spores produce 2-celled promycelia. At F the two lower cells in the chain are clearly uninucleated while the spores above are binucleated, but at E the basal cell is binucleated. In some forms scarcely a binucleated spore can be found in a sorus. At G is shown a very young sorus, and at H, a somewhat older one where from first to last the cells are uninucleated.

As noted, cell fusions regularly occur in the aecidium of the long-cycled orange-rust (Pl. 2, T). By triple or quadruple fusions, 3 and 4 nucleated spores presumably may arise as in the other rusts. What would this mean in germination and in infection? In forms of the short-cycled Caeoma rust with spermogonia where cell fusion would be expected to occur frequently, binucleated spores may possibly arise without such fusions. Then, too, 3-nucleated spores are not at all rare in these forms (Pl. 2, K). In strains without spermogonia and with uninucleated spores originating without fusion there are also 2-nucleated spores, possibly formed as the result of nuclear division and also from cell fusions. By studying stained preparations of germinating spores the writer becomes more thoroughly convinced that the orange-rusts represent forms which are not fixed in their life cycles. Bearing in mind the facts regarding the methods of origin of the aecidiospores one may understand more readily why there is such a great variation in the forms of promycelia.

96461—24†——7

NUCLEI IN PROMYCELIA

In Plates 3 and 4 are shown promycelia in various stages of growth from the germination of spores on to the formation of sporidia. The preparations studied were fixed and stained. The shaded areas merely represent living substance, cytoplasm and nuclei. The magnification is the same as used in Plate 2, which is somewhat higher than used in Plate 5, with which the figures should be compared. In Plate 3, A to K, are represented promycelia from spores of the rust on plant No. 497. At A and B division of the original nucleus has taken place; at C, the original nucleus has moved out into the promycelium where it will divide only once. The first cross wall is sometimes laid down before the first division (D), but most frequently division occurs in the spore itself. Any departure from standardized behavior on the part of the nuclei is reflected at once in the promycelium (J, K). In one case the promycelium has only two cells, but one of them has two nuclei. In the one shown at K there are three cells, with one, two, and three nuclei, respectively.

The other promycelia (Pl. 3, L to R), are from spores in aecidia of strains which produce spermogonia. It should be noted that spores which develop promycelia with three or more cells are correspondingly larger. At M is shown a promycelium with six cells, but only four of them are alive and nucleated, while at Q there is shown a 4-celled promycelium, one cell of which is dead, the other three contain two nuclei each. At N is shown a sporidium with three nuclei; one cell of the promycelium was dead. Perhaps its nucleus migrated into the upper cell and entered its sporidium. A binucleated sporidium arises as the result of division of its original nucleus, generally after the sporidium is matured.

Further details in the growth of promycelia are shown in Plate 4, A to J, from plant No. 489, where most of the aecidiospores are uninucleated. At A, the germ tube is put out before nuclear division, while nuclear division has already occurred in the spore shown at B. At C, the two daughter nuclei are passing out of the spore. Nuclear division is shown taking place in the promycelium at D. In cultures of this rust from plant No. 489 a great majority of the spores germinate in the forms shown from A to K. Figures L to S show types of germination from spores which had originally two or more nuclei. Three nuclei were clearly visible in the large spore shown at L. One nucleus in each of the cells of promycelia shown at M, Q, and O is degenerating. At N, two nuclei are entering the sterigma. The central cell of the 3-celled promycelium at S has two nuclei, the others, one each. Figures T to V in Plate 4 show the prevalent type of promycelium from the rust on plant No. 493. At X and Y are shown 4-celled promycelia, but it seems two cells in each case have captured the nuclei, three and three at X, two and four at Y. If the terms "normal" and "abnormal" must be used in describing promycelia, it should be done for convenience only, meaning by "normal" the most common or prevailing type. All of the odd forms could probably be looked upon as regular if one only knew the whole story. The writer has found aecidiospores with as many as seven nuclei in a young sorus whose spores were most regularly uninucleated.

DISCUSSION

The short-cycled orange-rusts of Rubus have much in common with those included under the genus Endophyllum. According to Hoffman (*4*), whose work has been confirmed by Moreau (*12*), cell fusions occur at the origin of the aecidiospore chains in *E. sempervivi*. The two nuclei resulting from the conjugate divisions of the nuclei contributed by the fusing cells, being cut off in the spore cell, fuse before the spore is shed. The fusion nucleus, which is much larger than either of the original nuclei, then undergoes a division so that the mature spore

again contains two. This first division may be delayed and later occur in the germ tube. The first septum is laid down before the second division occurs. Finally, a single uninucleated sporidium develops from each of the four cells. Such a course of procedure, following as it does what is known of nuclear behavior during the formation and germination of the teleutospore of the rusts, has been considered by some authorities to be sufficient evidence to warrant calling the aecidiospore of an Endophyllum a teleutospore. Evidence is accumulating very rapidly, however, to indicate that while the spore forms of the rusts as morphological entities are fixed because of their phylogenetic antecedents, the methods by which a particular spore form arises and the nuclear behavior at its origin and during germination are far from generalized, orderly, or fixed processes.

In the Florideae the methods of origin of the cystocarps and nuclear behavior in the cell activities involved in the formation of carpospores vary in some essential details with almost every genus in the five orders. One certainly must expect that their rust offspring will be just as individualistic.

There is an Endophyllum, *E. euphorbiae-silvaticae*, in which, as proved by Sappin-Trouffy (*14*) and Moreau (*12*), the two nuclei originally entering the aecidiospore never fuse. They pass out into the young promycelium and divide once, giving the four nuclei for the maturing of four sporidia. According to Maire (*10*), one of the two original nuclei of the spore of *E. valerianae-tuberosae* degenerates so that a reduction division could not follow.[4] Moreau (*11*, *12*) has furthermore given convincing proof that there is a form of *E. euphorbiae* with uninucleated aecidiospores and that there are no cell fusions in its aecidium. Her figures of the germinating spores and of the promycelia are, however, not all that could be desired. Whether or not Moreau believes that the promycelia from these uninucleated spores would "normally" be 4-celled and produce four spores is not clear from her papers. Nothing in her figures suggests such a thing.

Certainly one finds no explanation of the peculiarities of the orange-rust in *Puccinia malvacearum*, the only rust lacking spermogonia that has been thoroughly studied as to its cytology and physiology. It is a perfectly "normal" short-cycled form, except for its lack of spermogonia. In the absence of any definite knowledge respecting spore formation and the nuclear phenomena in those other rusts which lack spermogonia it would be futile to speculate on the meaning of the loss of these structures in the strain of *Caeoma nitens* under discussion.

Knowing nothing as to the development of spermogonia by the "*uninucleatum*" strain of Endophyllum, and nothing regarding the number of nuclei and cells in the promycelium except that the germ tubes that were obtained did have septa, it can only be said that further research may show that this Endophyllum may resemble the orange-rust not only as to the origin of its uninucleated spores, but also in the suppression of its spermogonia as well as in the formation of 2-celled promycelia. Germination of the spores of the form of *E. euphorbiae*, which Maire (*10*) claims becomes uninucleated by degeneration, should also be studied.

Two other European cytologists are accumulating evidence proving that life histories of species of rusts are not always as fixed events as has heretofore been generally believed. Kursanov (*7*) has pointed out that in certain sori of *Aecidium punctatum* the peridial cells and their interstitial cells are uninucleated. The spores in such a sorus are uninucleated except that here and there a spore has two nuclei clearly as the result of nuclear division. Nothing is said of the manner of germination of the uninucleated spores. There is a form of *Aecidium*

[4] In a later paper (MAIRE, R. L'ÉVOLUTION NUCLÉAIRE CHEZ LES ENDOPHYLLUM. Jour. Bot. [Paris] 14:80-97, 369-382, pl. 3. 1900) he figures 2-celled promycelia, failing to furnish any evidence by figures, that the aecidiospore becomes uninucleated by degeneration.

leucospermum which occurs frequently in the vicinity of Moscow and which Kursanov (*6*) finds has sori with chains of uninucleated aecidiospores. No cell fusions take place at their origin. The spores germinate like the ordinary aecidiospore, except that the germ tube has one nucleus instead of two. The spores with two nuclei are much larger than those with only one, whereas Moreau (*12*, p. *182*) found that the uninucleated spores of her Endophyllum corresponded in size with those described for the species. Occasionally a spore in one of the chains is binucleated. Such a case is clearly the result of a nuclear division. Where a chain of binucleated spores is found in a sorus the possibility of a cell fusion at the base is not precluded.

Lindfors (*9*) has more recently given a most interesting series of brief discussions of life histories of certain rusts. He has signally departed occasionally from the practice of trying to make what he finds in his material conform to the commonly accepted notions of cell fusions and to the doctrines relating to the fixity in rust cycles. For example, he finds that in *Uromyces acetosae* the first telia develop close to the aecidia. He figures an aecidium and a telium arising out of a common uninucleated mycelium. He also claims that the binucleated condition is not limited as to its origin, to cell fusions at the base of a sorus. Although cell fusions occur in *Puccinia arenariae*, without spermogonia, the promycelium has only two cells. Two binucleated sporidia are formed.

Up to the present time one of the greatest obstacles to the understanding of the workings of evolution in the Uredineae is our proneness to believe in the fixity of what are called genera and species. Owing to the immediate need for some systematic treatment of rust parasites, which were being discovered attacking our economic plants, much of the preliminary work, of necessity, has been based on dried material. Furthermore the cytological work has mostly been confined to a study of the so-called sexual fusions. The desirability of gathering, for fixation, material obtained as the result of extended culture work was clearly not of prime necessity in those days when Blackman and Christman were making their discoveries relating to nuclear migrations and cell fusions occurring at the origin of the aecidium. Moreau and Kursanov did not supplement their cytological work on uninucleated aecidiospores with culture work, and nothing was said regarding the presence or absence of spermogonia in those forms. Judging from Moreau's figures of the promycelia, which do not show any nuclei, it would not be surprising to find that if the uninucleated spores of that Endophyllum were germinated under conditions sufficiently normal to lead to the formation of sporidia, the promycelium would be found to be regularly 2-celled with one nucleus in each cell.

Blackman (*1*) saw in the sterile cell above one of the fusing cells the ancestral red alga trichogyne, and he saw in the migrating nucleus passing up into the basal cell (the "egg cell") a substitute for the now functionless spermatium. This view has long been discarded. In all of the more or less deep-seated aecidial primordia the fusing cells are in reality merely intercalary cells of the stroma-like, space-making, and food-storing hyphal plexus. The fusions are of exactly the same nature as are those occurring between the accessory sterile and auxiliary cells in the red algae. The resultant is the accumulation of materials and vigor for the building of numbers of reproductive spore bodies.

Christman's (*2*) suggestion that the cell fusions occurring between two equal cells must represent the sexual fusions of the ancestral Spirogyra-Mucor of the Conjugateae, while not generally accepted in this particular sense, nevertheless has gone far to establish firmly in the literature the terms sexual cells (gametes) and sexual fusions for those purely secondary fusions occurring between cells which have no homologies whatever to sexual organs, spermatia and oogonia, of any possible ancestral form.

There is no structure known in the rusts which takes the place of or is the homologue of an egg apparatus. The factor which stands for such an organ was either discarded when the rusts were evolved, or it became recessive to the extent that, for all that is known, the egg structure is always suppressed. It is this loss or impotency of the factor for that element of femaleness represented by the egg that distinguishes a rust most fundamentally from its ancestral alga.

The existence of a strain of any rust characterized by the development of a 2-celled promycelium has not hitherto been reported. Inasmuch as the suppression of spermogonia has been said in this paper to be so constantly associated with the production of uninucleated spores with abbreviated promycelia, it might appear as though the writer looks upon the production of spermogonia as inseparably connected with the faculty for initiating cell fusions. This may indeed be true to a certain extent, but, as has been noted, the development of spermogonia does not always insure cell fusions, for a few cases of infection have been found where, though spermogonia were present, the spores were uninucleated.

There is, of course, something in the inheritance of the rusts that determines when and where these cell fusions shall take place, as well as the nature of the cells fusing. The five great orders in the Florideae are distinguished mainly on the basis of the form and disposition of the carpogonial branches and auxiliary cells, and on the nature of the cell fusions which follow as secondary events. The gonimoblasts or ooblastema filaments, sporophytic outgrowths from the fertilized egg, in many genera are also involved in these secondary fusions preliminary to the development of carpospores. It is to these secondary cell fusions in which the auxiliary cells of the red alga take the leading part that we must look for the homologues of the rust fusing cells.

There being no organ such as an egg apparatus in the rusts, the spermogonia, though they are so well developed in many species, can not carry out their primary male sexual function. Nevertheless, there may be a series of activities in the growth of the rust bound up ("linked") with or influenced by the very inheritance which manifests itself morphologically in the shape of spermogonia. The fusions between the ooblastema filaments and auxiliary cells, and the other cell fusions in the red algae may very well be determined by the stimulus resulting from the presence of some of that element of maleness normally derived from the spermatium during fertilization. In the absence of the sexual fusions certain auxiliary cell fusions would not occur.

Femaleness in the red algae outwardly expresses itself primarily in the organization of the carpogonial branch bearing the egg cell and its trichogyne. Auxiliary cells are a secondary manifestation or accompanying phenomenon. In a dioecious alga one should not expect to find auxiliary cells borne on the male plant. Femaleness in the orange-rust—that is, the power to develop an egg apparatus—has been lost. Auxiliary cells represented by the cells in the sorus primordium are the secondary expressions. These cells are capable of fusing, usually in pairs, under a certain stimulus.

Maleness in the red algae is expressed in the form of antheridia (spermogonia) producing spermatia. These bodies function primarily in fecundation, and, in certain groups, secondarily in the cell fusions subsequent to fertilization. In the rusts maleness has persisted as shown by the development of spermogonia with their spermatia, which are primarily functionless in the absence of an egg apparatus. This condition is associated with the occurrence of accessory cell fusions, culminating in Gymnoconia in nuclear fusions in the teleutospore.

A long-cycled rust becomes short-cycled without losing the power to develop that morphological structure, the promycelium. A promycelium may be formed without there having taken place a nuclear fusion previously, in which case

obviating the necessity for a reduction nuclear division. For this reason the number of cells in a rust protobasidium need not always be four. The presence of some male element exercising its secondary function indicates maturity and cell fusions will occur, while inhibition of such a development is manifested by the omission of cell fusions.

Aside from the immediate developments dependent directly on fecundation, there is frequently a whole series of activities well known and recognizable in sexual reproduction in plants and animals which result from the expression of sexuality in a secondary capacity. One can conceive of such a thing as the agent inaugurating cell fusions in the short-cycled orange-rust being ordinarily "linked" with or dependent on the factor which stands for spermogonial development, yet occasionally becoming separated from this factor. Ordinarily then the appearance of spermogonia would be followed by cell fusions, except where there has been a transfer of the factors for fusions to some other determinant where it could no longer express itself normally.

The Gymnoconia as noted becomes short-cycled by omitting or suppressing the telial stage. If that combination of factors which was instrumental in bringing about a shortening of the life cycle were unconnected with maleness in any way, the rust would develop its spermogonia, cell and nuclear fusions would follow as before, and the spores would germinate with 4-celled promycelia. If one should be able to prove that in the short-cycled form there are no nuclear fusions and that chains of binucleated or multinucleated spores may arise without cell fusions, it would be further evidence of the complexity of the factors involved in the development of the various spore forms.

The writer has pointed out that the spores with one nucleus are smaller than than those with two or more. This agrees with what Kursanov (*8*) says of the uninucleated spores of *Aecidium leucospermum*. Kunkel (*5*) figures uninucleate aecidiospores of the short-cycled orange-rust, but he interprets them as resulting from nuclear fusions. It should be noted that in his figures the uninucleated spores are in both cases much smaller than the binucleated spores.

The very fact that promycelia with irregular or odd numbers of cells—three to nine are found—and that as many as five nuclei may occur in one cell, would indicate that this multicellular, multinuclear condition has not arisen as a result of fusions of nuclei in pairs in the aecidiospore followed by regular reduction divisions.

It is inconceivable that a 7-nucleated aecidiospore which was found in an aecidium, the other spores of which were mostly uninucleated, could have been the result of the fusion of seven cells. When such a spore germinates, a promycelium is formed which, from the nature of its origin, will be normal; but from a viewport fixed by previous misconceptions, will be abnormal. The writer has found that in certain strains of the short-cycled orange-rust practically every promycelium is 4-celled. This can almost be determined in advance by the form and size of the aecidiospores. In any culture where the spores vary considerably in shape and size some "abnormal" promycelia will be developed.

There is a rather fascinating hypothesis which might be brought forward to account for the frequency with which one finds the omission of the spermogonial stage is associated with the omission of cell fusions and with the production of 1-nucleated spores in the aecidium.

If as Kniep maintains in the anther smut, *Ustilago antherarum*, the two sporidia at one end of the promycelium are "plus" and the other two "minus," then the host can be infected so that the rust develops normally only when a sporidium of each sort takes part in the infection. Infection from a single sporidium might be possible only in case the strain happened to be capable of, say, an androgenetic development assuming that + and − refer to femaleness and maleness. In this

event, spermogonia would be formed, but cell fusions being omitted the aecidiospores would be uninucleated. If the sporidium from the opposite end produced infection it could only be by a gynogenetic process. In such an event, no spermogonia would appear, no cell fusions would occur, and 1-nucleated spores would arise.

The two strains evolved should remain or continue to be true to form, but by bringing about a double infection with a sporidium of each sort one would obtain a strain with spermogonia, cell fusions, 2-nucleated aecidiospores and 4-celled promycelia. The difficulty with which one is able to infect a blackberry systemically and the rareness with which natural systemic infections occur in comparison with the vast number of spores shed, would suggest that this hypothesis should not be entirely ignored. One is reminded that future infection work with the orange-rusts should be carried on with spores at least from a single plant and ultimately with single aecidiospores and even with single sporidia.

SUMMARY

Certain strains of the short-cycled orange-rust on Rubus do not develop spermogonia except perhaps as they are aborted or vestigial.

The aecidiospores in such strains are for the most part uninucleated. Binucleated or multinucleated spores are sometimes present in such aecidia.

Cell fusions do not occur at the origin of a chain of uninucleated aecidiospores.

The number of nuclei in an aecidiospore may be increased by nuclear divisions.

The size of an aecidiospore varies with the number of nuclei present at its maturity. The uninucleated spores are much smaller than those with two or more nuclei.

A spore with one nucleus germinates normally; its nucleus divides once so that a 2-celled promycelium which matures two sporidia is formed.

The number of cells in a promycelium and the number of sporidia matured is not fixed, but depends to a great extent on the number of nuclei in the aecidiospore. A polynucleated spore is very large and would probably give rise to a promycelium with more than four cells and very likely some of the cells would contain more than a single nucleus.

Degeneration of nuclei sometimes occurs in the cells of promycelia and certain of its cells may die, so that the number of sporidia eventually formed does not necessarily correspond to the number of nuclei originally present.

So far as yet observed spermogonia are always matured by the long-cycled rust *Gymnoconia interstitialis* and cell fusions occur.

Strains of the rust which commonly form 4-celled promycelia when the aecidiospores are germinated always develop spermogonia. In this form the binucleated aecidiospores arise as the result of cell fusions.

That nuclear fusions always occur in the aecidiospore or its promycelium in the short-cycled orange-rust is questioned.

So-called "abnormal" promycelia with other than the traditional number, four, cells are accounted for by nuclear behavior during spore development and germination. When a spore has but one nucleus, that nucleus divides only once during the formation of the 2-celled promycelium.

Binucleated spores arising from cell fusions usually develop 4-celled promycelia, possibly without nuclear fusions followed by reduction divisions. On this principle a precocious division of the nuclei in a spore followed by a multicellular promycelium need not introduce a new element into the inheritance of the rust.

LITERATURE CITED

(1) BLACKMAN, V. H.
1904. ON THE FERTILIZATION, ALTERNATION OF GENERATIONS AND GENERAL CYTOLOGY OF THE UREDINEAE. Ann. Bot. 18: 323–373, illus.

(2) CHRISTMAN, A. H.
1905. SEXUAL REPRODUCTION IN THE RUSTS. Bot. Gaz. 39: 267–275, illus.

(3) DODGE, B. O.
1923. EFFECT OF THE ORANGE RUSTS OF RUBUS ON THE DEVELOPMENT AND DISTRIBUTION OF STOMATA. Jour. Agr. Research 25: 495–500, illus.

(4) HOFFMAN, A. W. H.
1912. ZUR ENTWICKLUNGSGESCHICHTE VON ENDOPHYLLUM SEMPERVIVI. Centbl. Bakt. (II) 32: 137–158, illus.

(5) KUNKEL, L. O.
1914. NUCLEAR BEHAVIOR IN THE PROMYCELIA OF CAEOMA NITENS BURRILL AND PUCCINIA PECKIANA HOWE. Amer. Jour. Bot. 1: 37–46 illus.

(6) KURSANOV, L.
1913. SUR LA MORPHOLOGIE DES URÉDINÉES. Trav. Sec. Mycol. et Phytopathol. Soc. Bot. Russ. 1: 19–21, illus. [In Russian. French resumé, p. 19–21.]

(7) ———
1914. ÜBER DIE PERIDIENENTWICKLUNG IM AECIDIUM. Ber. Deut. Bot. Gesell. 32: 317–327, illus.

(8) ———
1922. RECHERCHES MORPHOLOGIQUES ET CYTOLOGIQUES SUR LES URÉDINÉES. Bul. Soc. Nat. Moscou (n. s.) 31: 1–129, illus.

(9) LINDFORS, T.
1924. STUDIEN ÜBER DEN ENTWICKLUNGSVERLAUF BEI EINIGEN ROSTPILZEN AUS ZYTOLOGISCHEN UND ANATOMISCHEN GESICHTSPUNKTEN. Svensk Bot. Tidskr. 18: 1–84, illus.

(10) MAIRE, R.
1900. QUELQUES URÉDINÉES ET USTILAGINÉES NOUVELLES OU PEU CONNUES. Bul. Soc. Mycol. France 16: 65–72.

(11) MOREAU, MME. F.
1911. SUR L'EXISTENCE D'UNE FORME ÉCIDIENNE UNINUCLÉÉE. Bul. Soc. Mycol. France 27: 489–493, illus.

(12) ———
1914. LES PHÉNOMÈNES DE LA SEXUALITÉ CHEZ LES URÉDINÉES. Botaniste 3: 145–284, illus.

(13) OLIVE, E. W.
1908. SEXUAL CELL FUSIONS AND VEGETATIVE NUCLEAR DIVISIONS IN THE RUSTS. Ann. Bot. 22: 333–360.

(14) SAPPIN-TROUFFY, P.
1896. RECHERCHES HISTOLOGIQUES SUR LA FAMILLE DES URÉDINÉES. Botaniste 5: 59–244.

(15) WERTH, E., and LUDWIGS, K.
1912. ZUR SPORENBILDUNG BEI ROST- UND BRANDPILZEN. Ber. Deut. Bot. Gesell. 30: 522–528, illus.

PLATE 1

A to E.—Types of orange-rust on Rubus

A.—Short-cycled, spermogonia and four-celled promycelia. Waxy spores heaped up in the sori.

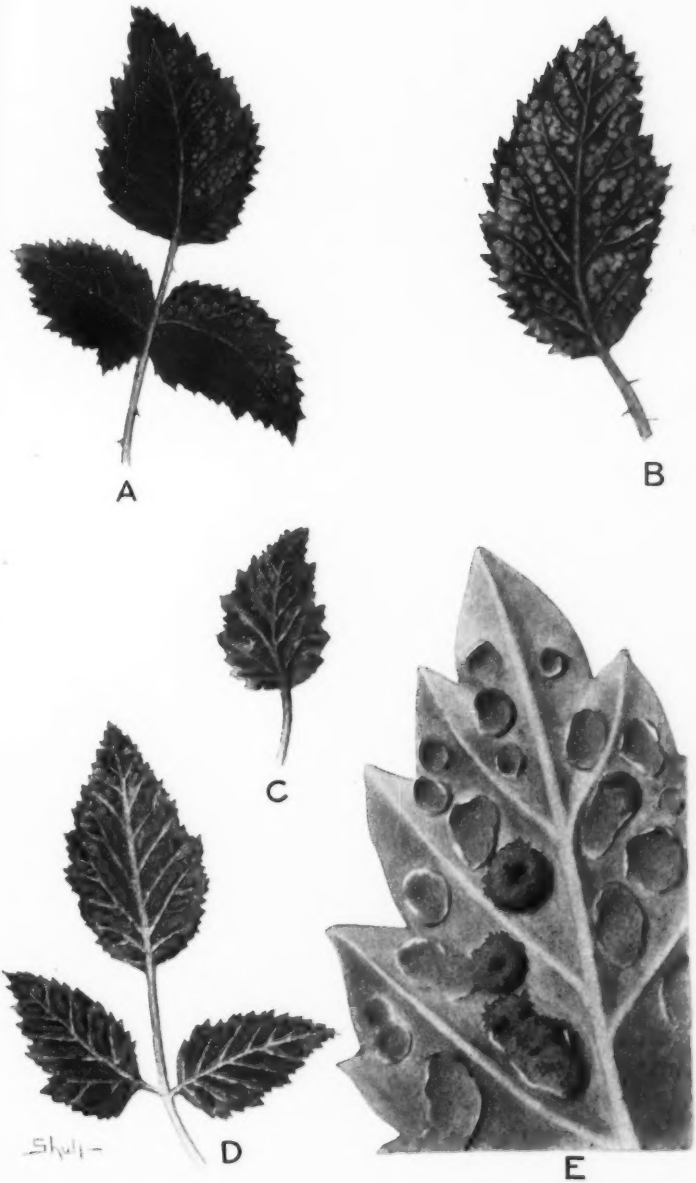
B.—Short-cycled, no spermogonia, 2-celled promycelia. Yellowish spores waxy.

C.—Three yellowish short-cycled sori like those in B, other sori long-cycled.

D.—All sori long-cycled.

E.—Light orange empty sori, long-cycled; reddish orange sori with waxy spores are short-cycled. Two long sori partly short-cycled and partly long-cycled. x 12.

B. C. and D from the same plant.


A
B
C
D
E

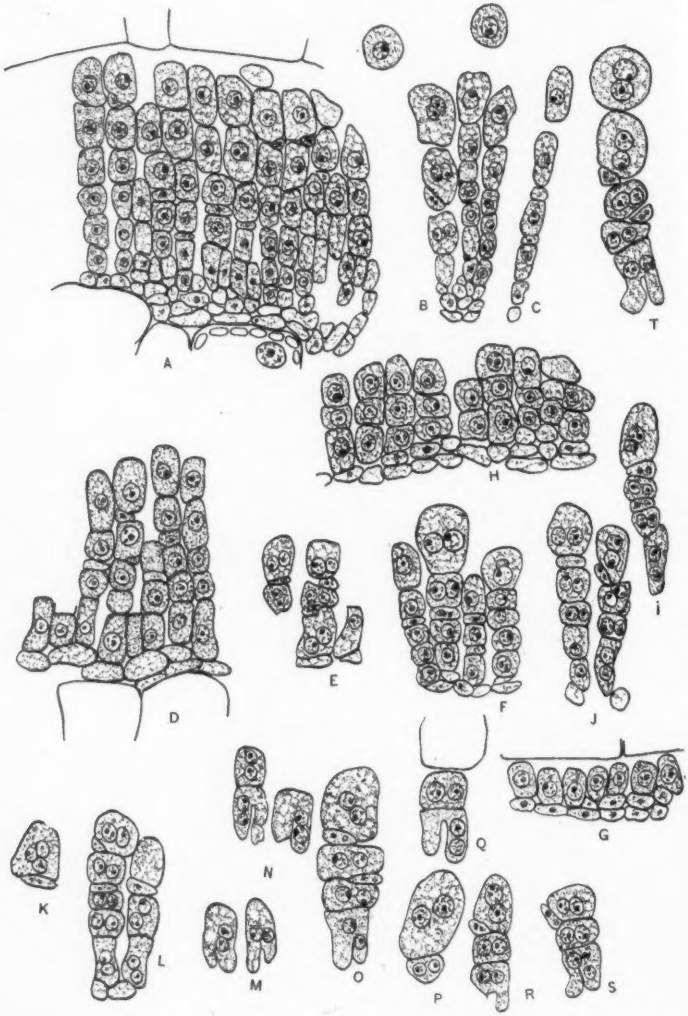
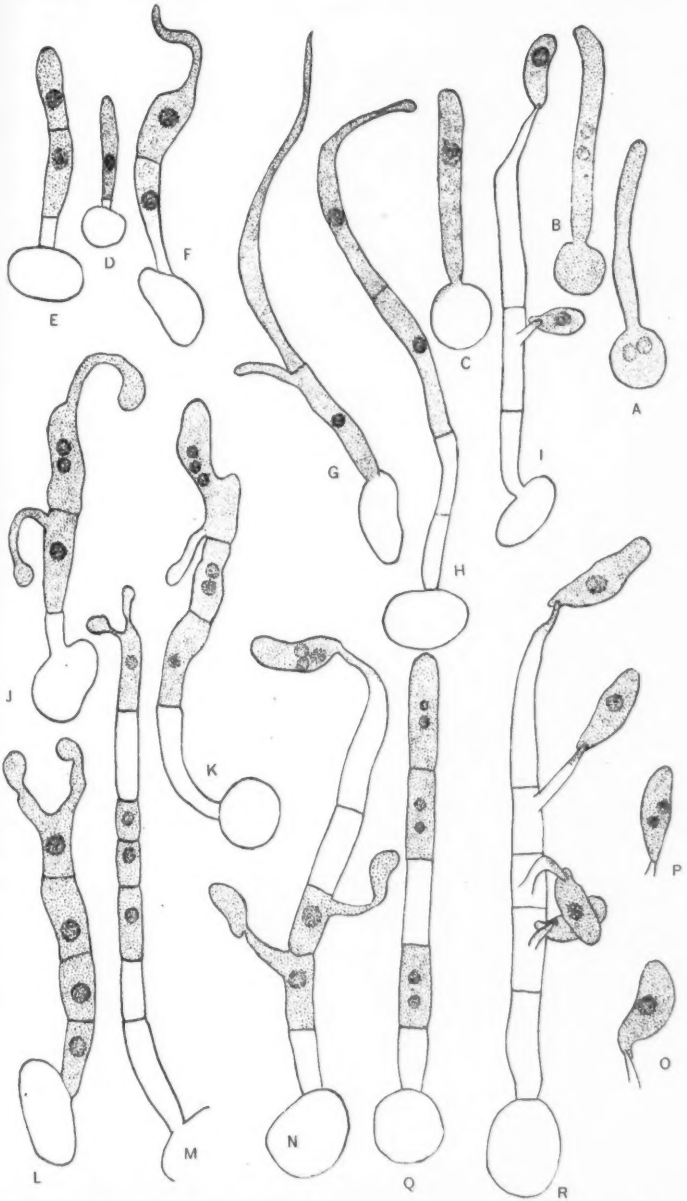

A
B
C
T
H
D
E
F
J
i
G
Q
N
K
L
M
O
P
R
S

PLATE 2

A to C.—From sections of a young aecidium on Crandall blackberry. No Spermogonia, no cell fusions, mostly 1-nucleated spores. D to F.—Spore-chains from aecidium on plant No. 497. G.—A young primordium. H.—Older sorus; all cells 1-nucleated. I to S.—From strains maturing spermogonia. T.—Spore-chain from the long-cycled Gymnoconia on *Rubus occidentalis*

PLATE 3

A to J.—From the short-cycled rust on plant No. 497 (cf. Pl. 5, A to I). K to R.—From strains producing spermogonia


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R

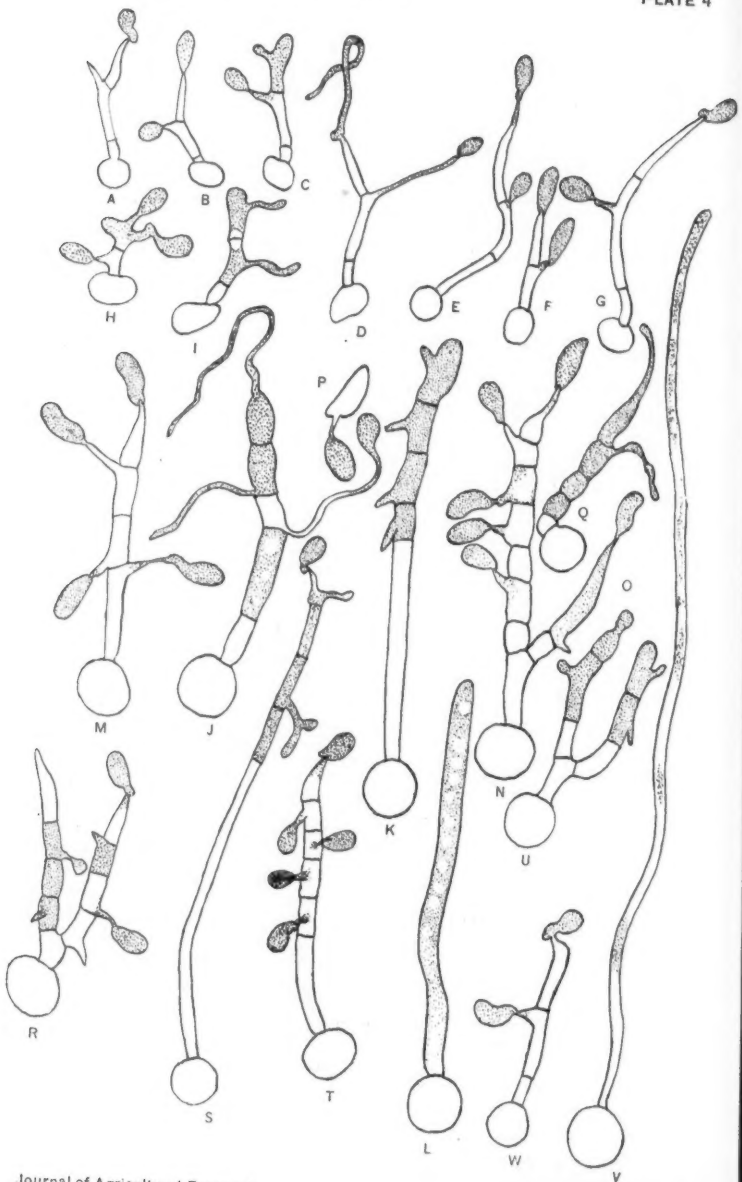

A
B
C
D
E
F
G
H
I
P
M
J
K
Q
O
N
U
R
S
T
L
W
V

PLATE 4

A to Q.—From short-cycled rust on plant No. 489. R to Z.—From a strain of the short-cycled rust on plant No. 493

PLATE 5

A to I.—2-celled promycelia from germination tests from plant No. 497. Small spores slender promycelia. J to V.—Promycelia from strains which develop spermogonia. Cells without cytoplasmic contents not shaded. W.—2-celled promycelium from a strain having spermogonia and 1-nucleated spored.

Uninucleated Aecidiospores in Caeoma nitens

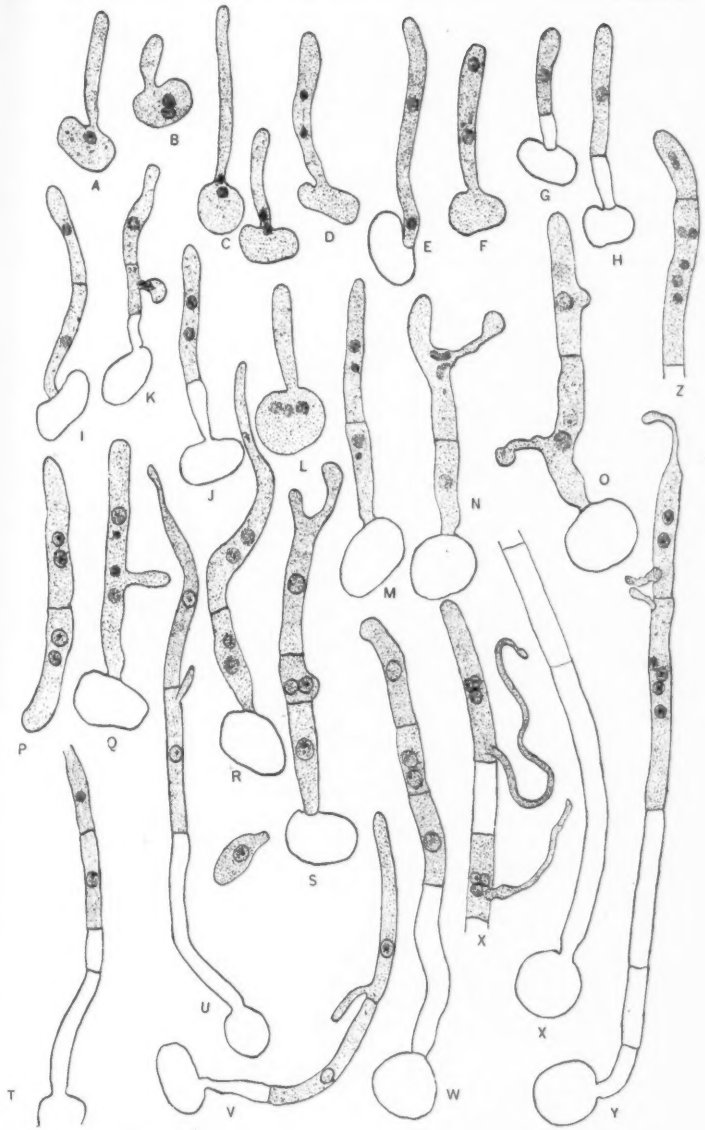



PLATE 5